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FRONTAL SINUS EVOLUTION (PARTICULARLY IN THE EQUIDAE)

By Tilly Edinger

With Nine Plates

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I. ACKNOWLEDGEMENTS

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II. THE EQUUS CONDITION

Pneumatic spaces occupy large areas in the head of the adult common horse. They are the three pairs of paranasal cavities: the sphenopalatine, maxillary, and frontal sinuses.

The body of the sphenoid contains a cavity halved by an irregular median osseous septum. The *sphenoidal sinus* continues laterally into the palatines (fig. 3C), or there are separate *palatine* sinuses.

A *maxillary sinus* pneumatizes the posterior region of each upper jaw. Its main portion usually lies over the two posterior molars, and it never reaches farther forward than over M^1. The anterior limit of its more dorsal portion is always the infraorbital foramen, the vertical, slit-like opening of the canal which runs horizontally forward from the orbit, within the sinus. Expanding during ontogeny, the maxillary sinus spreads into the lacrimal and zygomatic bones. Thus it extends along the front wall and floor of the orbit (fig. 1). The posterior ends of the maxillary sinuses present a graphic example of a sinus characteristic, variability. In the cross-sectioned skull described below, a posterad[1], tapering diverticle pneumatizes the anterior half of the suborbital shelf. The corresponding left side diverticle, however, is wider and hollows the entire shelf. Thus it hollows practically the entire zygomatic bone — it tapers out where the zygomatic narrows to a slender tongue underlying the zygomatic process of the temporal bone. Ontogenetic expansion of the maxillary sinus is also brought about by the progressive extrusion of M^2 and M^3, so that in old horses the maxillary sinuses are the largest of the three pairs; length varies from 125 to 185 mm., breadth from 60 to 85 mm. (Baum 1894).

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[1] The Latin suffix -ad, expressing a direction toward, does not seem to be generally used in the American scientific language, particularly not to form adjectives, but its use has simplified the present paper's descriptions of cavities extending, during ontogenies and phylogenies, in this and in that direction.

The right and left frontal sinuses are separated only by a double sheet of bone, the septum sinuum frontalium, whose thickness varies around 1 mm. The pair constitutes the largest pneumatic area in the horse skull. Among the numerous detailed investigations of these cavities, those based on the most material are those of Goubeaux 1852, Baum 1894 (66 skulls of 5-to-15 year-olds), and Bressou 1919 (40 fresh heads and 43 skulls, from 4 years to very old); a more recent one is Anthony 1929, and shorter descriptions are found in textbooks such as Sisson 1940. These studies have established the following conditions in the adult common horse.

Each frontal sinus lies primarily between the tabulae externa and interna of the frontal bone. Laterally it extends into the supraorbital (zygomatic) process of the frontal. Posteriorly it may reach almost to the fronto-parietal suture (14% of Bressou's cases). Anteriorly it has a dorsal extension into the nasal bones. Laterally, too, it continues beyond the frontal bone — along the ethmoidal labyrinth, roofed in by the lacrimal, nasal, and maxillary bones. Its osseous floor is interrupted by a wide opening, up to 45 mm. long and 35 mm. broad (pl. 1 = fig. 8, f.m. — a communication with the maxillary sinus. Anterior to this there is a tapering anterad section of the frontal sinus. This extends into the posterior part of the dorsal (naso-) turbinate bone. It is anteriorly closed off, by a transverse wall, from the anterior part of the dorsal turbinate (which part alone functions, with scrolls, as a nasal turbinate). This anterior extension of the sinus is often called pars turbinalis sinus frontalis. Sinus nomenclature varies considerably, depending on the importance an author attributes to the connections of the sinuses — with each other, with the nasal cavity, and between the compartments of each sinus. The present study is not concerned with such details as these communications and subdivisions.

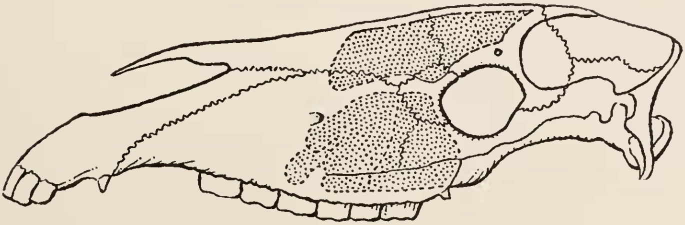


Fig. 1. *Equus caballus.* Topography of left frontal and maxillary sinuses. After Bressou (slightly changed). ⅙ nat. size.

Although Bressou found that the frontal is that sinus whose dimensions vary least, its variability in shape and size is nevertheless great and is strictly individual. At least from the 4-year-old on (the youngest horse studied in this respect), variation is neither related to age, nor to the slight variations in skull roof profile, nor to skull size, nor are the right and left frontal sinuses of one head necessarily similar. In Baum's material of 530 to 600 mm. long skulls, the diameters of the frontal sinus varied as follows (1894, p. 166–169): length, 130–200 mm.; height, 55–80 mm.; breadth, 55–80 mm. Greatest height and breadth were found to occur in approximately the same transverse plane.

None of the descriptions summarized above gave me a full picture of the actual position of the frontal sinus, namely, a picture including the relation of the frontal sinus to the structural units it adjoins within the horse skull. I studied this, particularly, in two skulls of adult horses. No. I (MCZ, Mammal Dept. No. 1713) is 580 mm. long and shows wear of all 3 premolars; it is halved sagitally close to the median plane, so that in one half the septum sinuum hides the sinus — the sinus of the other half is shown in fig. 9. Paramedially, the sinus is 92 mm. long; laterally, 160 mm. No. II (MCZ, Mammal Dept. No. 43500) is 560 mm. long, has the first premolar and some of the second worn, and was transversely sectioned across the posterior region of the orbits. In this specimen (pl. I, fig. 8) I broke away the dorsal outer plates of the frontal bones and explored the sinus in detail. Shooting this horse in the forehead had destroyed the anterior sinus extensions. Maximum breadth of the sinus pair is 150 mm. The greatest depths are 53 mm. on the right and 46 mm. on the left side; they lie 1–2 mm. anterior to the plane of greatest width.

This transverse region of greatest sinus volume passes about 10 mm. behind (not "vor" — Baum 1894, p. 168) the posterior extremity of the dorsal rim of the orbit. Naturally, the sinus has its greatest width where it extends into the postorbital processes. All figures in the literature locate the lateral end of the frontal sinus at any odd place between the root of the postorbital process and the postorbital foramen; only Hamoir describes and figures the orbital diverticulum as continuing laterad behind the foramen (1918, p. 412 and fig. 4).

Both the sinus of my No. I specimen which can be probed and the left sinus of II end laterally with a tapering tip in the postero-dorsal rim of the postorbital foramen. They seem to come to an end at a naturally given point (a point not reached by the right sinus of II): the proximal wall of the supraorbital foramen. This so-called foramen is in *Equus* rather a canal. It perforates perpendicularly the postorbital process which at this point is 10 mm. high. The minimum lumen of the canal is 5 mm., its funnel-like dorsal exit is 9 mm. in diameter.

From braincase to canal the postorbital process is a voluminous structure; by the canal it is divided into two smaller units, which join distal to the canal to form a comparatively slender bar. The postorbital diverticulum of the frontal sinus ends just proximal to the canal's greatest width. The canal thus appears to set a natural limit to the laterad extension of the frontal sinus, particularly as this condition recalls the configuration at the anterior end of the maxillary sinus, which always coincides with the infraorbital foramen.

Immediately proximal to the supraorbital canal the left sinus of II has a groove in its floor so that it is here, near its lateral end, still a 15 mm. high cavity. This groove is not developed on the right side; there the sinus floor, from next to the supraorbital canal, slopes evenly proximad towards the greatest depth of the sinus. The sinus floor in this region is formed by the outside wall of the cranium under, and just behind, the postorbital process; it is to some extent orbital, mostly temporal fossa wall.

Neither measurements nor figures can convey the real picture of the region of greatest sinus depth. Figures in the literature show either a side view like our fig. 1, or a section. The longitudinal section always chosen to demonstrate the frontal sinus is that next to the septum sinuum frontalium (our fig. 9). However, the deepest pocket of the sinus floor is neither lateral nor median in the skull, but intermediate in position. It is in a situation which appears to be fixed by the topography of the brain capsule.

It is in fact impossible to reproduce in the two dimensions of an illustration the impression obtained upon removal of the sinus roof, that practically horizontal, even sheet of bone which at first sight, in a whole skull, seems to be the entire frontal bone but is only the tabula externa ossis frontalis. It roofs a vast empty space: the frontal sinus. The sinus is irregularly halved by the more or less median, more or less perpendicular septum sinuum frontalium. The curves of the lateral and posterior outlines of this cavity are interrupted by irregular diverticula, or rather by the septa between them, which jut into the sinus perpendicularly, obliquely or even (from the left orbit of II) horizontally, in straight or sinuous fashion. Yet a major part of the sinus floor has a very definite shape. This is in the main and posterior regions of the sinus, and is the real roof of the anterior brain cavity, shaped by the brain.

Medio-sagittal sections of the skull (fig. 9) show the sinus in the sagittal plane of its shortest anter-posterior extent. In this section, next to the septum, the sinus appears triangular. The "base" of the triangle is in the skull roof; the "apex" is below in a transverse furrow of the braincase roof. Below this furrow, inside the braincase, is the dorsal contact of cerebral hemispheres and olfactory bulbs. The transverse furrow on the dorsal, sinus-side of the braincase corresponds to the furrow, on the dorsal surface of the brain, between cerebrum and bulbi. The transverse ridge on the endocranial surface of the frontal bone which contains the part of the sinus here described is, so-to-speak, a septum dorsally separating the two brain portions. Its lower rim frames, from above, a pair of intracranial perpendicular windows, in which the cerebro-olfactory contact takes place. These windows (see fig. 7C) apparently have not been named; they may be called ethmoidal or olfactory windows. From the transverse paramedian furrow which indicates the position of these windows on the dorsal surface of the braincase, to the skull roof above, the sinus is 35mm. high in the No. I specimen, 38 mm. in II.

Anterad from here the sinus floor rises over the roof of the ethmoidal chambers (fig. 8, O.) and the nasal cavity until it joins the skull roof, that is, the tabula externa of the nasal bone. Lateral from these paramedian cone-shaped portions the sinus cavities are continued much farther forward. There is a large section pneumatizing the orbit roof and wall. Here there is, in the floor from at least the middle of the orbit forward, the wide-open connection with the maxillary sinus, and the sinus walls are more lacrimal and maxillary than frontal bone. Beyond the anterior end of the orbit is the turbinate extension, topographically part of the nose; it lies between the maxillary sinus and the vaulted dorsolateral roof of the muzzle.

Lateral from the region above the ethmoidal windows the sinus floor drops to its deepest point (fig. 8, P.). There the right sinus of II is 53 mm. deep, the left one 46 mm. This pair of basal pockets are 59 mm. distant from each other, symmetrically situated, immediately lateral to the cerebro-olfactory windows inside the braincase, and thus immediately in front of the anterior extremities of the cerebral chamber. They are funnel-shaped, their outside walls being in the basomedially-slanting lower region of the cranium walls.

In all the descriptions of frontal sinuses which I have read, I found just one reference to such basal pockets. Lechner writes [1](1932, p.277): "Near the median septum the sinus floor has a groove which extends farthest basad, but does not reach the sphenoid wings. This recess lies lateral to the ethmoidal fossa. It might be called a hollow stem on which rests the frontal sinus like a funnel-shaped pyramid. Lateral to it the sinus is considerably more shallow and juts out into the beginning of the zygomatic process". It is the skull of *Felis domestica* which Lechner describes. Such pockets are shown in Paulli's figure of a cross-sectioned cat skull (1900, fig. 17) but are not mentioned in Paulli's

[1] I have translated foreign language quotations.

text. They are no doubt frequently present in pneumatized mammal skulls, and they are a significant feature.

In *Equus caballus,* at least, position and shape of the widest sinus region appear to be determined by position and shape of the ethmoidal and cerebral chambers. This fact, incidentally, may be the reason why in horses a laterad diverticulum may reach behind the postorbital foramen but has never been observed anteriorly. There is as much or more room for sinus expansion within the postorbital process anterior to as posterior to the foramen; but it is the posterior portion of the process which continues laterad the plane between ethmoidal and cerebral chambers.

Posterad from this transverse region of greatest breadth and depth, the floor of the sinus is the wall over the anterior slope of the cerebral hemispheres (fig. 8, C.). Its squarish outline and its profile mirror those of the frontal region of the cerebrum; its prominences correspond to the impressions of frontal brain gyri in the ventral side of this inner plate of the frontal bone, and the grooves in this portion of the sinus floor correspond to cerebral sulci. Thus the sinus here envelops, dorsally and laterally, the anterior region of the cerebral cavity. Its breadth is fairly uniform, 72 mm., from the anterior poles of the cerebral chambers to about 30 mm. behind them. The sinus thus extends over the whole breadth of the anterior cerebrum.

There follow posterad what Bressou (1919, p. 275) describes as diverticulations at the posterior extremity of the frontal sinus. Rather, in this region each sinus tapers concomitant with the gradual approach towards each other of the outer cranial wall and the braincase. In our specimen whose whole sinuses are laid open (fig. 8), the "median" septum turns to the right so that the left sinus has become, at its posterior end, a practically median and symmetrical formation. This posterior end is rounded, and the point of greatest posterad extent is only 3 mm. to the left of the midline of the skull. Next to it, the sinus is still 15 mm. broad and 5 mm. deep. The right sinus tapers similarly in depth and breadth, but ends 10 mm. more anteriorly. Thin perpendicular walls of compact bone close these sinus extremities against the spongiosa which lies between the tabulae externa and interna posteriorly — viz., where the dorsal surfaces of skull and cerebrum are close to each other and are parallel.

These posterior regions of the frontal sinuses are stated in the literature to be particularly variable in posterad extent. Bressou describes this be saying that the sinus ends between 20 and 60 mm. behind a line connecting the *posterior extremities of the orbits* (1919, p. 275; Hamoir's surgical study uses the same orientation, 1918, p. 412). Baum reports that the caudal end of the sinus lies in one transverse plane with the *anterior border of the lower jaw articulation* or up to 10 mm. anterior to this, and thus one or two fingers' breadth behind the *zygomatic process of the frontal bone* (1894, p. 166). Such connecting of the end of the frontal sinus with distal skull regions — distant and unrelated to the sinus, and perhaps themselves variable — hardly illustrates the posterad extent of the sinus which, to us, appears determined by the shape of the *braincase*. We find that in brain morphology lies the reason why in one individual the sinus reaches farther posterad than in another individual.

The sinus floor follows the cerebral surface posterad up its anterior slope to the horizontal brain surface, where it ends. The sinus variations are not greater than, in fact they correspond to, the variations of that brain region. The frontal lobe of *Equus* has an anterior facies of very variable steepness. Adjoining the olfactory bulbs, the profile is perpendicular up to variable heights; this is followed posterad by an upward slope of variable length. The horizontal part of the dorsal surface of a cerebral hemisphere thus begins at different distances from the anterior poles. It is at this variable location that there remains no gap between the tabulae externa and interna, and each sinus comes to a brain-determined posterior end. This is particularly well illustrated in our specimen II in which the left sinus extends farther back than the right and into the medial area; its tapering, symmetrical extremity follows to the end the symmetrical anterior slope of the cerebrum.

Bressou remarks (1919, p. 275) that there is nothing which allows one to predict, nothing which explains the variations of frontal sinus capacity in the horse. Our observations restrict the scope of this statement to the anterior regions, whose irregularities, like those of the dorsal and lateral sinus borders, are minor variations characteristic of sinus formation. As regards both the vastest and the posterior regions of the frontal sinus, it is the variations of the anterior profile of the brain which are unpredictable and unexplainable, but they account for the sinus variations.

Thus the sinus frontales, twin cavities in the middle region of the horse skull, occupy the spaces between

1. dorsally, the skull roof;
2. laterally, the side walls of the skull forming and adjoining the orbits;
3. medially and basally, (a) the posterior region of the nasal cavities, (b) the ethmoidal chambers which contain the olfactory bulbs of the brain, and (c) the anterior region of the cerebral cavity with that part of the cerebrum whose dorsal surface slopes anterad.

Further, the frontal sinus continues anteriorly into a non-nasal turbinate cavity, and in its transverse plane of greatest depth and breadth it extends into the postorbital process.

As the different lengths of the postorbital diverticulum suggest, this extension of the frontal sinus grows laterad even during adult life. Paulli's pl. IX (1900; briefly referred to p. 191, p. 249) shows in side view the skull of a newborn foal with the sinuses laid open; the frontal sinus reaches no farther posteriorly than to the transverse plane connecting the anterior borders of the postorbital processes. No special study seems to have been made of the ontogeny of the frontal sinus in the horse, but of other mammals it is well known that pneumatization increases in extra-uterine life at least as long as the skull grows. Weidenreich has culled from the literature the facts that in calves, kids and elephants the frontal bone is not pneumatized at birth (1924, p. 82). The "very young", 308 mm.-long skull of a giraffe shows no trace of pneumatization, at least not in a sagittal section of the frontal and parietal bones (Lankester 1907, fig. 29); both these bones are highly pneumatized in adult giraffes (our fig. 7C). Ghetie (1941) studied the sinuses of the pig in a series of skulls which included those of very young and very old individuals. Of the eleven sinuses which this author distinguishes, the youngest pigs have only the maxillary sinus. Next to appear is a cavity in the anterior and lower regions of the frontal bone (loc.cit. p. 171, p. 174), the future "fronto-occipital sinus". All sinuses were found to expand up to old age (p. 171).

Several studies of maxillary sinus development in ungulate embryos, while not mentioning the frontal sinus, attest to the fact that the latter develops later than the former. The recessus which is the Anlage of the maxillary sinus (an epithelial tube long preceding bone formation) appears in pigs in a 25 mm. embryo (Dennhardt 1903, p. 13), has a closed lumen in the 28 mm. embryo (p. 14), and the "turbinate sinus" is first seen in the 34 mm. stage (p. 18; the sphenoid sinus is not mentioned). In Dennhardt's sheep material, maxillary and turbinate sinus Anlagen are present in the youngest, a 34 mm. embryo. The frontal bone Anlagen, however, are described as "solid" (p. 35) in the oldest pig and sheep embryos studied, 160 mm. and 100 mm., respectively.

In horses (Sörensen 1934) the lumen of the future maxillary sinus first appears in the 27 mm. embryo (p. 625), and sphenopalatine and turbinate sinus Anlagen appear in the 180 mm. embryo (p. 630). The oldest embryo (290 mm.) has the maxillary sinus similar to that of an adult, except for size, and it reaches the orbit (p. 632–633); but there is no trace of a lumen in its frontal bone Anlage, at least not in the regions shown in Sörensen's figs. 12 and 13.

When and how did this voluminous structure of the head of the horse appear in the series of adult ancestors of the extant form?

The numerous special investigations of the *Equus* paranasal sinuses do not even speculate upon this question. Their viewpoints are veterinary — with particular regard to surgery —; or they compare the anatomy of extant mammals, or are purely descriptive. In the large literature on the fossil ancestors of *Equus* there seems to be only one reference to skull sinuses, and this is a case of mistaken identification.

When the evolution of the equid brain was studied from *Hyracotherium* (eohippus) to *Equus* (Edinger 1948), observation of the circum-cerebral skull regions revealed that no frontal sinus existed when the Equidae evolved from the common ungulate stock in the Lower Eocene.

III. THE EQUID FOSSIL RECORD

1. Description

Hyracotherium (Lower Eocene). Numerous fragments were studied of *Hyracotherium* skulls belonging to the Museums listed on p. 412, the Carnegie Museum, Pittsburgh, Pa., and to Dr. Horace Elmer Wood of Rutgers University at Newark, N. J. The broken surfaces of these fragments expose sections of frontal bones in a variety of places. Nowhere was a pneumatic space discovered within the frontal.

The specimen chosen to illustrate the structure of *Hyracotherium* frontal bones is the fragment of the *H. venticolum* muzzle AMNH 14810 which is figured in its entirety in my 1948 paper, fig. 4. It is prepared so as to lay open the matrix in the nasal tunnel, in the right ethmoidal chamber, and in the anterior cerebral cavities. The bulk of the left frontal bone is left in situ (with, perhaps, the adjoining nasal bone region); the right frontal bone is sawed off 1.5-2 mm. from the median suture. Natural breakage has produced three sections through the bone:

1. anteriorly, a crooked transverse section. This is the irregular border of the bone as preserved. Above the ethmoidal labyrinth the frontal bone is paper-thin, slightly thicker more medially over the ethmoidal chamber as seen at the right end of fig. 10.

2. posteriorly, a transverse section through the roof of the cerebral chamber near (5 mm. behind) the anterior poles of the hemispheres. This section (fig. 11) shows conditions inside the frontal bone in a transverse plane 4-5 mm. behind the posterior border of the postorbital process. There is a thin tabula externa, a thicker tabula interna, and between the two a layer of cancellate bone.

3. laterally, an approximately sagittal section through the root of the left postorbital process. In this section the process is triangular;

the perpendicular posterior border is 5 mm. high, the anteriorly converging borders each are 4 mm. long. Thin compacta encloses a nucleus of spongiosa.

The 4th section is an artificial one, that made by the saw, paramedial through the right frontal (fig. 10). It includes the roof of the most anterior slope of the right cerebral hemisphere; the ventrad transverse ridge of the frontal between cerebral and olfactory bulb chambers; and the anterior tapering portion of the frontal which overlies olfactory chambers and ethmoidal labyrinth. Thus this section includes the transverse plane of greatest frontal bone thickness which is in *Equus,* as we have seen, the plane of greatest frontal sinus depth. In *Hyracotherium,* however, only a transverse septum is formed by the endocranial side of the frontal bone. While triangular in paramedian section like the corresponding formation in *Equus,* it is a different structure. From the "base" in the skull surface, the apex of this triangle reaches down 6 mm. into the skull. The same measurement of greatest frontal bone thickness was obtained in a *Hyracotherium validum* specimen (YPM, VP-11694; this natural endocranial cast, with the skull base *in situ,* is 20 mm. high medially in the plane where cerebrum and olfactory bulbs adjoin, while the plaster cast taken of this skull before the roofing bones were removed is here 26 mm. high). As is seen in fig. 10, throughout this region, too, only tiny-celled cancellate tissue intervenes between the compact inner and outer plates of the frontal bone. It follows that the frontal sinus proper was not developed in *Eohippus.*

On the other hand, a maxillary sinus existed. In *Hyracotherium* the orbit is above the posterior grinders, not posterior to the teeth as in *Equus.* The floor of the orbit seems to overlie the teeth closely in undamaged maxillaries, such as the right one of the AMNH muzzle. From the left maxillary of this specimen a perpendicular break has removed the last molar tooth. The transverse section of the jaw thus revealed is plastered over laterally, but above the medial part of M^2 shows a once empty space, now stone-filled. It is 5 mm. high, its medial bone wall about 3 mm. thick. This cavity is not the infraorbital canal; on the right side of the specimen this canal is seen to end in the orbit in a plane much anterior to our section. The cavity above the M^2 can be interpreted only as a pneumatic space, a maxillary sinus.

Mesohippus (Middle Oligocene). Scott (1891) figured a longitudinally sectioned *Mesohippus* skull together with one of *Equus* (pl. XXIII, figs. 17 and 18). It must have been the result of direct comparison of the two that Scott designated the dorsal ante-cerebral chamber — a chamber in the area which in *Equus* is part of the frontal sinus — as the frontal sinus of *Mesohippus* (p. 406.--Ibid.

p. 307 and Scott 1941, p. 915: "The frontal sinus is but little developed and does not extend over the brain at all"). However, the endocranial casts of *Mesohippus* show that the chamber in question is the ethmoidal; the space was occupied by the olfactory bulb when *Mesohippus* was alive. Scott's figure, incidentally, is not a good reproduction. The specimen itself (Princeton University no. 10503) shows that the figured surface of the right skull half is the mediosagittal plane. The ostensibly lateral, 21 mm. long process coming down from the skull roof is actually in the plane of section; it is the longitudinally sectioned median ridge (ethmoidal crest) between right and left ethmoidal chambers.

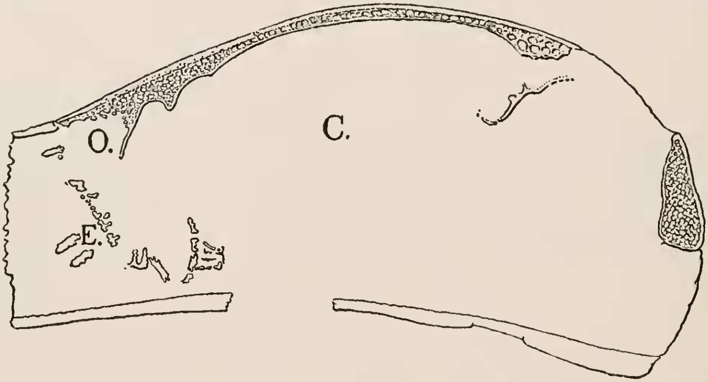


Fig. 2. *Mesohippus* sp. (M.C.Z. 6594). Right half of skull fragment, paramedian section. Nat. size.

In the sectioned surfaces of both right and left halves of this skull the frontal bone is seen to consist of rather thick tabula externa, small-celled cancellate layer and thin tabula interna. In the right skull half, the matrix is removed from the cerebral chamber so that the transverse ethmoidal window is revealed. Its upper rim is about horizontal, 10 mm. below the outer surface of the frontal bone. The left half of the skull shows that the region in which the frontal bone is thickened to form, with its inner plate, the roof of these windows, is 15 mm. long.

Mesohippus MCZ 6594 supplements the data gained from the Princeton specimen, as this skull is longitudinally sectioned not medially but just to the right of the midsagittal plane. It therefore shows in section the frontal bone above and between the right cerebral and ethmoidal chambers (fig. 2). There was an 8 mm.-deep transverse septum sloping down over the anterior cerebrum. Its lower part is very thin. This condition had been suggested by the endocranial casts, in all of which much of the olfactory bulbs is closely applied to the cerebrum. Only the upper 5 mm. of the septum is thicker and contains cancellate tissue. Anteroposteriorly the thickened part of the frontal bone is 23 mm. long. Posterior to the septum proper one sees the tabula interna protrude into the two transverse sulci on the anterior surface of the cerebrum. Of these two juga cerebralia, the anterior one is constructed like the septum, but the posterior one is in the zone of posterad tapering of the thickened region. Anterad, this region tapers so that over the anterior part of the olfactory bulbs there is hardly 1 mm. of bony roof.

The cross-sectioned *Mesohippus* skull, Princeton University no. 11114 (fig. 3, A, B; the sectioning destroyed about 1.5 mm. between these two surfaces), shows the olfactory bulb chambers 3–5.5 mm. anterior to the cerebro-olfactory septum. It is seen that these ethmoidal chambers were not, as in *Equus*, deep within the skull, but immediately adjoined the skull roof. This consists of frontal bone with but a narrow layer of spongiosa. Likewise, the lateral wall of the ethmoidal chamber was cranial wall, namely, the pars orbitalis ossis frontalis: a dorsal portion of the medial wall of the orbit. This is not preserved in the endocast preparation shown in fig. 3; but in other *Mesohippus* specimens it can be seen, not pneumatized as in *Equus*, but as a 1 mm.-thick sheet of bone between orbit on the outside, olfactory bulbs and ethmoidal labyrinth on the inside.

It thus appears that there was no pneumatization anywhere in the frontal bone of *Mesohippus*.

The *Mesohippus* upper jaw fragment MCZ 17659 was cross-sectioned at the posterior end of M^2. The section shows the infraorbital canal, and lateral to this, above M^2, an 8 mm.-wide maxillary sinus.

Miohippus (Upper Oligocene). A *Miohippus* specimen loaned to me for brain study (from Princeton University; no. 11127) was a braincase when received. To reveal the endocranial cast, the bones were chipped off and thus do no longer exist. It was noted that over the posterior region of the olfactory bulbs and over the anterior cerebral region each frontal bone contained an extensive nucleus of cancellate tissue. The spongiosa cells were larger along the median plane than laterally, and larger also than any seen in *Mesohippus*. Unfortunately the depth of the frontal bone was not measured.

Parahippus (Lower Miocene). In the *Parahippus* skull fragment MCZ 17878, "A mass of cancellate frontal bone, more extensive in every direction than the corresponding region in the frontal bone of

Miohippus, was removed in search of the olfactory bulbs" (Edinger 1948, p. 70). It was then recorded that the thickness of frontal bone matter was 23 mm. between the cerebral and ethmoidal chambers, and 14 mm. above the highest vault of the latter. We have preserved in fragments much of the bone chipped off in this preparation, and left

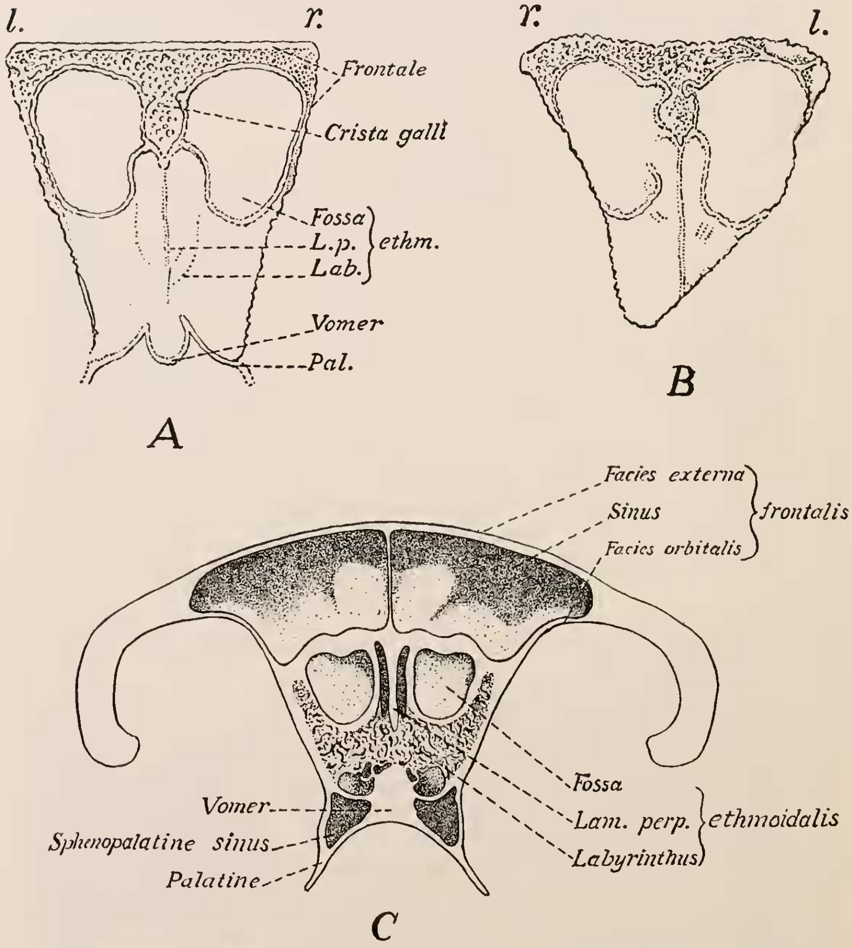


Fig. 3. A, B: *Mesohippus* sp. (P.U. 11114). Approximately transverse section across olfactory chambers (fossae ethmoidales); A: distal, B: proximal side. 1½ x nat. size. C: *Equus caballus.* Distal side of skull sectioned across olfactory chambers and postorbital bars. After Baum. ⅜ nat. size. (From Edinger 1948.)

in situ the cranium along the midline and over the left cerebral hemisphere, plus some of the tabula interna frontalis covering the olfactory bulb casts. Thus this specimen contains many sections through the frontal bone. Nowhere was a pneumatic cavity discovered.

The longitudinal section of the frontal over the right cerebral hemisphere (13 mm. from the midline) is typical of the relatively thin areas, such as is also the roof of the posterior orbit; over the vault and the anterior slope of the cerebrum, the external compacta is ± 4 mm. thick, the internal compacta much thinner, and there is a 2–4 mm.-high layer of spongiosa. The cross section above the cerebro-olfactory furrow shows the typical thick region; below the 4 mm.-thick outer plate is an irregular layer of small-celled spongiosa, and the wide area below this, down to the thin inner plate, is occupied by coarse, wide-celled spongiosa.

Thus the structure of the frontal bone is basically the same throughout, in thin and in very voluminous regions. This early representative of the *Parahippus* group had no frontal sinus.

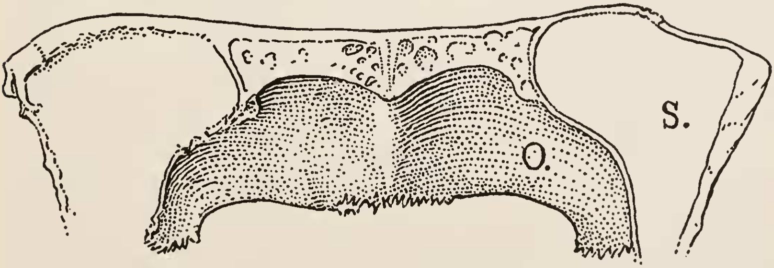


Fig. 4. *Merychippus* sp. (A.M.N.H. 32671). Frontal bone broken over olfactory chambers, anterior view. 2 × nat. size.

Merychippus (Middle and Upper Miocene). A Middle Miocene skull roof fragment and a broken neurocranium from the Lower Upper Miocene show that in *Merychippus* frontal sinuses were developed.

Merychippus sp., AMNH 32671, from the Sheep Creek beds, is a portion of a braincase roof which ends anteriorly in an irregular break (fig. 4). In this crooked cross section can be studied medially the structure of the frontal bone above the posterior part of the ethmoidal chambers. Laterally the break runs backward on either side towards the plane of the ethmoidal windows, thus sectioning the frontal also at its greatest thickness. Here, there was found a pair of lateral compacta-lined spaces in which there is nothing but matrix: remnants of frontal sinuses. Their endocasts are 11 mm. deep, but the sinuses were deeper, as the casts are broken on the lower side of the specimen. In ventral view this break has a subcircular outline, with about 4 mm. diameter. There were, consequently, pits in the sinus floor lateral to the ethmoidal chambers as in *Equus*. Cancellate tissue is seen on the left side of the transverse section only in the relatively thin bone over the ethmoidal chamber vault. Above the right ethmoidal chamber, loss of inner plate material has laid open more of the interior bone structure in this paramedian region. It seems that each frontal bone was filled with spongiosa to a breadth of 10 mm. outward from the median suture; that, consequently, the frontal sinuses were lateral only, separated by about 20 mm. of cancellate tissue. The specimen discloses neither how far the sinuses extended nor, of course, their rostrad extent.

The *Merychippus* sp. neurocranium AMNH 9393 (Pawnee Creek beds) ends anteriorly in an irregular series of breaks. In the cross break of the left frontal bone are seen, (1) cancellate tissue 14 mm. broad lining the dorsal outer plate, about 4 mm. broad laterally, 10 mm. broad next to the inner plate, and (2) enclosed by these spongy regions, an ovoid posterad groove, 10 mm. across and 5 mm. high, which is lined with smooth compact bone. This was the posterior end of the left frontal sinus. It is a cavity situated above the anterior slope of the left cerebral chamber and thus posterior to the section exhibited in the Middle Miocene specimen; the sinus extended farther back in the larger and later than in the smaller and earlier *Merychippus*.— On the right side of the Upper Miocene specimen the dorsal plate of the frontal bone is plastered over at the break; but on this side the neurocranial side wall is preserved farther forward than on the left side. It includes the lateral wall and a posterior part of the roof of the olfactory bulb chamber. Two more items relating to the frontal sinus are revealed here. Where the ethmoidal chamber adjoins the cerebral chamber, its roof, i.e. the tabula interna of the frontal bone, is 10 mm. below the tabula externa. Further, this tabula interna is as smooth dorsally as it is ventrally where it covered the olfactory bulb. Consequently, no cancellate matter lay over at least the latero-posterior part of the ethmoidal chamber, but a frontal sinus.

2. Interpretation

As demonstrated by the material described on the preceding pages, maxillary sinuses were present in the oldest of the ancestors of the horse, 55,000,000 years ago, whereas frontal sinuses were not developed before the Middle Miocene, 20,000,000 years ago.

Conditions in extant Mammalia have previously suggested that maxillary sinuses are "the original form of pneumaticity in the Placentalia" (Paulli 1900, p. 561). The oldest Equidae substantiate the conception that, as the neo-zoologist puts it, "the oldest form of pneumaticity in placental mammals is the maxillary sinus of the insectivores" (loc. cit., p. 559).

The origin of additional pneumatization has been variously explained on the basis of recent materials. Only one of these generalizations is interesting at the present point of our special study of the formation of a sinus in one phyletic series. This theory concerns the form of the skull. Frontal sinuses are supposed to be related to the formation of superstructures such as horns, forehead, crests. But the Equidae never developed superstructures — on the contrary; *Hyracotherium* had the parietals and frontals crested, and the crest was reduced to a vestige as the skull enlarged. Apart from this reduction and a greater increase in length of its facial than its cranial part, the skull has generally preserved the same appearance from *Hyracotherium* to *Equus*. In particular, there was always a practically flat skull roof.

It therefore seems that the changes which in the Equidae originated the frontal sinus took place in relation to intracranial structures.

We have seen that the frontal sinus proper of *Equus* is the space between level skull roof, anterior slope of the cerebrum, olfactory bulbs, ethmoidal labyrinth 7, and orbit. We have further located the oldest frontal sinus in the history of the Equidae between skull roof, cerebrum and bulbi. Going back to the earlier Equidae, we find that the space thus occupied did not exist in the earliest forms.

The origin and evolution of this intra-cranial space is illustrated by the numbers given in our table of perpendicular measurements in the skull region which lodged the olfactory bulbs and, in the later forms, also contains part of the frontal sinus.

The bulbi of *Hyracotherium* were relatively large formations anterior to the cerebrum, where they occupied the entire breadth and practically the entire height of the cranium (Column I). The skull roof likewise fitted on the cerebrum whose dorsal profile was a low curve. The inner plate of the frontal bone did, of course, protrude downward where it had to separate cerebrum and bulbi. However, it formed no more than a low, narrow transverse crest (column II; see fig. 10). The antero-posterior diameter of this crest is ventrally only 1 mm. The crest protrudes into the skull interior for only about one-fifth of the skull height (column IV).

Table of perpendicular skull measurements in the olfactory bulb region.

I. Thickness of frontal bone above highest vault of ethmoidal chamber (the chamber which contained the olfactory bulb).

II. Thickness of frontal bone paramedially at ethmoidal window (through which ethmoidal connects posteriorly with cerebral chamber).
III. Total skull height in the same place as II (dorsal surface of skull roof — facies frontalis ossis frontalis — to ventral surface of palate).
IV. Ratio of II (= 1) to III.

		I	II	III	IV
Hyracotherium	YPM, VP 11694	3	6	26	5.2
	AMNH 14810	2	6	28	4.7
Mesohippus	PU 10503	2	10	35	3.5
	MCZ 6594	1	8	30	3.8
Merychippus	CMNH 26032	—	18	56	3.1
Equus	Pony	(34)	l. 35, r. 33	83	2.4
	I	—	49	108	2.2
	II	34	41	110	2.7
	III	—	44	113	2.5

The bulbi: cerebrum height ratio remained basically the same during the evolution from *Hyracotherium* to *Mesohippus*. Correspondingly, the structure of the frontal bone in the region which was later to contain the widest part of the frontal sinus did not change; only small-celled spongiosa intervenes between outer and inner plates of the *Mesohippus* frontal bone. Directly above the vault of the olfactory bulbs the bone is even absolutely thinner than in two of the three *Hyracotherium* specimens measured (the Yale specimen and one in Dr. H. E. Wood's collection). The anterior cerebrum, however, had in *Mesohippus* a somewhat steeper profile, with a low vertical part (fig. 2). Correspondingly, the septum between cerebrum and bulbi gained relatively more in depth (col. II) than the skull increased in height (col. III). While still a small and inconspicuous structure, its share in the skull height has become larger (col. IV; I may add here two approximate figures I obtained from the *Mesohippus* endocranial casts AMNH 9768 and MCZ 1811. I "replaced" the destroyed external facies of the frontal bone by laying over these brains a thin ruler, and measured downwards from this "skull roof". Septum depths must have been about 10 and 12 mm., respectively, skull heights 42 and 45 mm., the ratios 4.2 and 3.8).

The one endocranial cast known of *Miohippus* revealed no noticeable progress in brain evolution over *Mesohippus*. Correspondingly, only cancellate tissue lay between the outer and inner plates of the frontal bones in *Miohippus*.

The *Parahippus* skull AMNH 14305, whose cerebral chamber has previously been described (Edinger 1948, p. 67), unfortunately lacks all intra-cranial structures anterior to the cerebrum. These were studied only in the MCZ skull and endocast 17878, Upper Lower Miocene in age. A considerable change was observed to have occurred in the topography of the olfactory bulbs since the Upper Oligocene. The upper vault of the bulbi was no longer close to the external surface of the skull roof. Above the bulbi the frontal bone was of considerable thickness. It contained in a coarse spongiosa large diploic spaces. A sinus was not developed, at least in this one representative of the genus *Parahippus*.

From an early member of the *Parahippus* group of species evolved *Merychippus*, the form which in our series of material showed the first sinus in the frontal bone. Within the genus *Merychippus* occurred important evolutionary changes. In the skull, the elongation of the muzzle began, high-crowned teeth developed, and the cerebrum assumed a modern appearance.

Up to the *Parahippus* stage, the equid cerebrum was more or less egg-shaped, with a low slope at its tapering anterior extremity. In both Middle and Upper Miocene *Merychippus*, the trend towards the sub-quadrangular shape seen in most *Equus* cerebra became manifest in broadened frontal lobes which, vaulting antero-dorsally, developed a definite anterior facies.

In the Middle Miocene, olfactory bulbs could still reach high up in the skull. They did in the specimen shown fig. 4; the frontal bone was only 5 mm. thick above the bulbi. On the other hand, a *Merychippus* endocranial cast of the same age (Chicago Natural History Museum no. P.26032) has the vault of the bulbi about 22 mm. lower than that of the cerebrum. The incomplete Upper Miocene cranium described above suggests an intermediate condition viz., 10 mm. difference. The Upper Miocene natural cast AMNH 8105, while not containing the bulbi, shows the anterior profile of the cerebrum rising steeply from the impression of the ethmoidal windows.

Certainly in *Merychippus* generally the cerebrum, and particularly the frontal lobes, rose to far greater height within the skull than the bulbi. One might say that, in a sense, the antero-dorsal bulge of the cerebrum lifted the tabula externa up and away from the tabula interna in the anterior part of the frontal bone. The inner plate now roofs ethmoidal chambers which do not continue the axis of the cerebral chambers, but lie on a lower level; it roofs ethmoidal windows along an inferior region of the cerebrum. The bulbi have, so-to-speak, evacuated the space anterior to the upper regions of the cerebrum. Between the tabula externa, which roofs the skull, and the tabula interna, which roofs, clings to, and is shaped by the brain, a space has evolved which has no function whatever. Bone substance, however, develops only under static or mechanical demand (Weidenreich 1924, p. 57). We have noted that the frontal bone spongiosa was loosened in *Parahippus*; the non-functional spaces between its osseous substance were larger than in the Oligocene Equidae, but still occupied by bone marrow. Weidenreich's reasoning led him to believe that there is, in principle, no contrast between diploic spaces and the pneumatic sinuses of the skull (1924, p 73); the latter are only larger (1924, p. 74). The history of the equid frontal bone shows that this is true. In the transition from *Parahippus* to *Merychippus* a diploic area became a sinus. With the vaulting of the anterior cerebrum in *Merychippus*, there originated within each frontal bone a larger superfluous area. The spongiosa was withdrawn. The empty space was walled off against surrounding diploë by the lamellar compacta whose smooth surfaces in our *Merychippus* specimens have been described above. These compacta walls, the typical lining of pneumatic intra-cranial spaces, show that the empty areas were air-filled; connection with the respiratory tract had been established, and the Equidae had acquired paranasal sinuses in the frontal bones.

I have not studied the skull interior of the evolutionary stages between *Merychippus*, in which at least a pair of dorsolateral frontal sinuses was developed, and *Equus*, in which the site of this original equid frontal sinus is the region of greatest depth and breadth of much enlarged, medially almost meeting sinuses. Of the intermediate stages of horse evolution, however, a number of endocranial casts have been studied. Certain trends observed in post-Miocene brain evolution were bound to further remove from each other the tabulae interna and externa of the frontal bone. Maximum cerebral height, which in earlier phases had increased at a slower rate than length and breadth, now gained relatively more than the other diameters. Frontal lobe vaulting increased, so that cerebral height gained anteriorly even more than posteriorly. The ratio of olfactory bulb height to maximum cerebral height, which had been 1:1.5 in *Eohippus*, was found to have fallen to 1:2.8 in one Pleistocene and two Recent *Equus*, and to 1:3.0 in a Shetland pony. Thus today the inner plate of the equid frontal bone has to reach far down into the skull to framet he ethmoidal window (see table, col. II; "Equus III" is the no. II specimen of my 1948 paper). The proportion between the depth of the frontal bone at the ethmoidal window and total skull height has fallen almost to half that in *Hyracotherium*, viz., an average of 1: 2,45 (col. IV). That is, medially and paramedially in this plane the frontal bone occupies two-fifths of the height of the large *Equus* skull, and laterally much more.

In the brain, the height increase of the frontal lobe was accompanied by considerable increase in breadth. Average maximum cerebral breadth has about doubled from *Mesohippus* to *Equus*, but average frontal lobe breadth became almost threefold. Nothing comparable happened to the olfactory bulbs. Their breadth increase corresponded rather to that of the posterior cerebral regions, while the greater breadth increase of the anterior cerebrum widened the anterior cranium. Thus occurred the discrepancies between inner and outer plates of the frontal bone which we have described, in the first chapter, as the main region of the frontal sinus. In *Hyracotherium* the lateral wall of the bulbus chamber consisted of inner *and* outer plate of the frontal bone. In *Mesohippus*, too, the lateral wall of the bulbus chamber was median orbit wall. In *Merychippus* (fig. 4) and in *Equus* there is a gap between the tabula interna protecting the bulbus olfactorius and the tabula externa protecting the bulbus oculi; and this gap is pneumatized.

The writer now feels obliged to make a paleontologist's apology. As usual, the number of fossil specimens on which this study is based cannot be compared to those the veterinarians have used to describe the frontal sinus of *Equus*. Of course, fossil equid skulls which happen to be broken or sawed in such a way as to lay open internal structure of the frontal bone are — the phrase is particularly appropriate — few and far between. I admit that the fossil material at hand does not even disclose the full extent of the frontal sinus in the one form of which all available details were described, *Merychippus*. Only the posterior sinus region is represented in our material of this genus. Variation within the sinus is shown, as the sinus reaches farther back over the cerebrum in an Upper Miocene than in a Middle Miocene specimen.

The differences recorded between the frontal bones of the different genera in the ancestral series of the horse, however, appear greater and more significant than the frontal bone and sinus variations of living horses.

The material showing these different evolutionary phases has been objectively described in section III, 1. The phases have been interpreted in the present section as they appear to one who may be prejudiced through having previously studied in detail, of all evolutionary changes in the phylogeny of the Equidae, only those of the brain.

We must therefore now consider the general interpretations which comparative anatomists have given to the occurrence of frontal sinuses. These neozoologists, too, are handicapped; for none has ever traced the actual evolution of a sinus; they derive their ideas from conditions existing today.

IV. CAUSES OF FRONTAL SINUS FORMATION

1. Theories

Frontal sinus formation is related to body size. In every ontogenetic development, and in at least the Equidae in post-Miocene phylogeny, the larger the skull becomes the greater are the areas invaded by air. However, this general principle is not all-explanatory. It cannot explain why the Equidae had to reach *Merychippus* size before developing frontal sinuses. Extant ungulates far smaller than *Merychippus* (and even the hyrax) have frontal sinuses. Pneumatization is more extensive in sheep and oxen than in deer of corresponding size. This difference is at least in part related to the fact that antlers are only attached to, but horns enlarge the skull, and the frontal bone in particular. Sectioned ruminant skulls such as seen in figs. 7C and 26 suggest that the horns are not the reason for the occurrence of the frontal sinus, but are pneumatized by the extension into them of sinuses already formed in the skull proper (this is the actual process in ruminant ontogeny). Large frontal sinuses develop in skulls with no superstructures at all — for example, the horse skull.

Pneumatization of superstructures, of course, makes them lighter. Sinuses have been believed to develop with the purpose of enlarging the skull without weight increase, so that the skull can retain a proper proportion to a large body and can accommodate the attachment of large muscles. Many an external feature, such as a vaulted calvarium, has been attributed to this supposed activity and purpose of sinuses — that is, to the air which fills it. Even the position of the eye has been regarded as influenced by such intra-cranial air. The orbit of the fossil equid *Hypohippus* is in a relatively low position "owing to the development of large frontal sinuses", according to Scott (1895, p. 97; see our p. 484). Actually, the position of the orbit is one of the several primitive features which *Hypohippus* had retained from its ancestors.

Paranasal sinuses are widely believed to have an olfactory function — to develop particularly in macrosmatic mammals, providing additional olfactory surface; but they never contain olfactory epithelium. Because in many mammals turbinal scrolls come to be lodged in the sphenoidal sinus, accommodation of such plates has been regarded as the primary significance of all pneumatic chambers; empty sinuses were seen as a secondary condition, due to reduction of the olfactory apparatus. One theory not only explained the occurrence of sinuses but also accounted for the fact that they enlarge during ontogeny; the gradual bending of the turbinal lamellae was supposed to compress and narrow certain arteries so that the bone marrow, insufficiently nourished, atrophies and gradually disappears, leaving empty spaces within the bones. Further, sinuses have been thought to have an auxiliary function in respiration and to enlarge through the pressure of air blown inward at breathing. In the opinion of Weinert, frontal sinus formation is similar to that of bone crests, namely, always caused by muscles; muscles "tear the bones apart" (1926, p. 404). These theories can probably neither be proven nor disproved by Recent or fossil data; they are certainly not supported by any feature in the history of the Equidae.

No theory accounts for the extreme differences in occurrence, shape and size of frontal sinuses between the different forms of mammals except that of Weidenreich (1924; summarized and documented with further evidence 1941, and 1943 p. 164-166). Weidenreich's is an interpretation of paranasal sinuses which takes into account the other cranial structures; it has been tested by comparisons of different extant members of several groups of mammals; and it is, as will be seen, applicable to the actual story of a frontal sinus we have investigated, that in the Equidae.

According to Weidenreich, the paranasal sinuses have no active function but are passively created dead spaces. Their shape and size are determined by the disposition of the adjoining structures. These are, first of all, the basic components of the skull — osseous structures whose shape and size are determined by the organs they serve. They are the brain capsule and the three constituents of the face: orbits, nasal tunnel, and tooth apparatus with palate. A 5th structure is the skull surface; this not only unites the parts into a whole and serves as a base for the head musculature, but also develops weapons and other superstructures.

Rarely do these elements of the skull blend harmoniously with each other in the extant higher mammals. Mostly, they are incongruous. Consequently, there are within the skull spaces not occupied by its basic components.

An example of one kind of such spaces happens to be shown in section in our fig. 2, *Mesohippus*, and fig. 5, hippopotami. It is the area between the posterior slope of the braincase and the nuchal plane. Concurrent with the stress of the nuchal muscles, this space is filled with cancellate bone (the same diploic space in *Equus* as in *Mesohippus*, but about eight times as thick antero-posteriorly).

If, however, unoccupied skull areas are not under stress, no bone develops to fill them. Their emptiness allows them to become invaded by air: to become paranasal sinuses. As to the role of size in pneumatization: "The larger the individual elements of the face, the greater, of course, is the incongruity between them and the larger the interspaces, that is to say, the sinus" (Weidenreich 1941, p. 389).

It follows that sinus formation is dependent not on one factor, but on several factors: the developmental trends of the different elements of the skull. It is clear that the driving forces at least of frontal sinus formation must have been differently distributed among the skull constituents in the different phylogenies of the living mammals. That pneumatization arose independently in each order was concluded even from the extant conditions (Paulli 1900, p. 562). Paleontology might be able to differentiate between the forces through which originated the basal spheno-palatine, the latero-basal maxillary, and the dorsal and lateral frontal sinuses, respectively. Speaking of the relations between frontal sinus, orbits and brain in the extant mammals, Weidenreich remarked that "the existence or absence of the frontal sinus apparently also depends on other factors difficult to analyze in each case" (1941, p. 389). Such analysis should be possible in ancestral series, where the actual evolution of a sinus can be traced from fossil ancestors through to the Recent condition.

2. Some extant cases

We are here concerned with the frontal sinus but should mention in passing that practically all living mammals have maxillary sinuses. It is the only sinus of the Insectivora and Chiroptera. Its very early appearance in pig and sheep embryos has suggested that the maxillary sinus is "a very old heirloom of the mammals" (Dennhardt 1903, p. 48). Perhaps "placentals" should be substituted for "mammals". No maxillary sinus has been found in monotremes and in some of the marsupials. It is reported to be absent, further, in the hippopotamus, whales, seacows, and pinnipeds. One is inclined to regard these latter cases as representing secondary conditions; but proof of this would have to come from fossil material.

Small bats have no pneumatization in their skull which is a tightly fitting capsule of the head organs; *Pteropus* has a maxillary sinus extending into the lacrimal bone and has no cavity in the frontal bone. This is also the condition in the Insectivora and the majority of rodents. The lack of pneumatization in sirenian skulls may appear as a special case, due to their pachyostosis; giant size does not change the condition — Brandt's classic on *Rhytina* repeatedly stresses the fact that these giants had neither frontal nor maxillary sinuses (1846, p. 32; 1861-69, p. 40). However, the Pinnipedia too, in skulls otherwise similar to those of the Fissipedia, lack pneumatic spaces, as do the Cetacea. The latter case is interesting with regard to the relation between high cerebral hemispheres and frontal sinus which we believe to have observed in the Equidae. Whale brains are almost spherical; but there is no frontal sinus. This goes to show that a feature related to sinus formation in one phylogeny has no effect in another; also, that some cases remain obscure if one tries to understand the pneumatization conditions of all the living mammals without knowing the evolutionary history of their frontal bone region.

Man, with a higher brain than the apes, has smaller frontal sinuses: his eyes are closer to the brain. The discrepancies between inner and outer plate of the apes' frontal bone further depend upon size and position of a superstructure lost in man, the torus supraorbitalis (Weidenreich 1924, p. 72). The paragon of a pneumatized superstructure is the dome of the elephant's head. Its surface serves the mighty nuchal and trunk muscles; in this case the major force driving apart inner and outer plates is — it all happens in extra-uterine ontogeny — expansion of the skull surface (Weidenreich 1924, p. 67). In Cavicornia horn formation lifts up the tabula externa far beyond the horn base region (figs. 7 C and 26). The ox skull, comparable, except for its characteristic superstructures, to the horse skull, has far larger frontal sinuses. However, the high layer of air cells in the frontal bones of pigs, too, continues — as in oxen — into the parietal and occipital bones. The pig condition is considered by Weidenreich (1924, p. 68) as parallel to that of the elephant; nuchal musculature, elongated burrowing muzzle and tusks require abutments which the braincase cannot provide without superstructures.

The pigmy hippo (*Choeropsis*) also has large frontal sinuses (fig. 5A), but those of the giant among the living Suina, *Hippopotamus*, are relatively much smaller. Weinert (1925, p. 267) has even declared that in *H. amphibius*, in contrast to *Choeropsis*, "Das Stirnbein . . .ist völlig massiv". This erroneous statement rested on the Milne Edwards figure reproduced in our fig. 5 B and on one skull investigated which must have been medio-sagitally sectioned like Milne Edwards' specimen. The latter author, too, found large sinuses in the pigmy and no trace of a sinus in the giant hippo (1868-1874, p. 51). The fact is that the sinuses of *Hippopotamus* cannot be seen in medio-sagittal skull sections, because they are lateral only (the hippo skull exhibits the condition suggested for *Merychippus* by our material). Paulli described

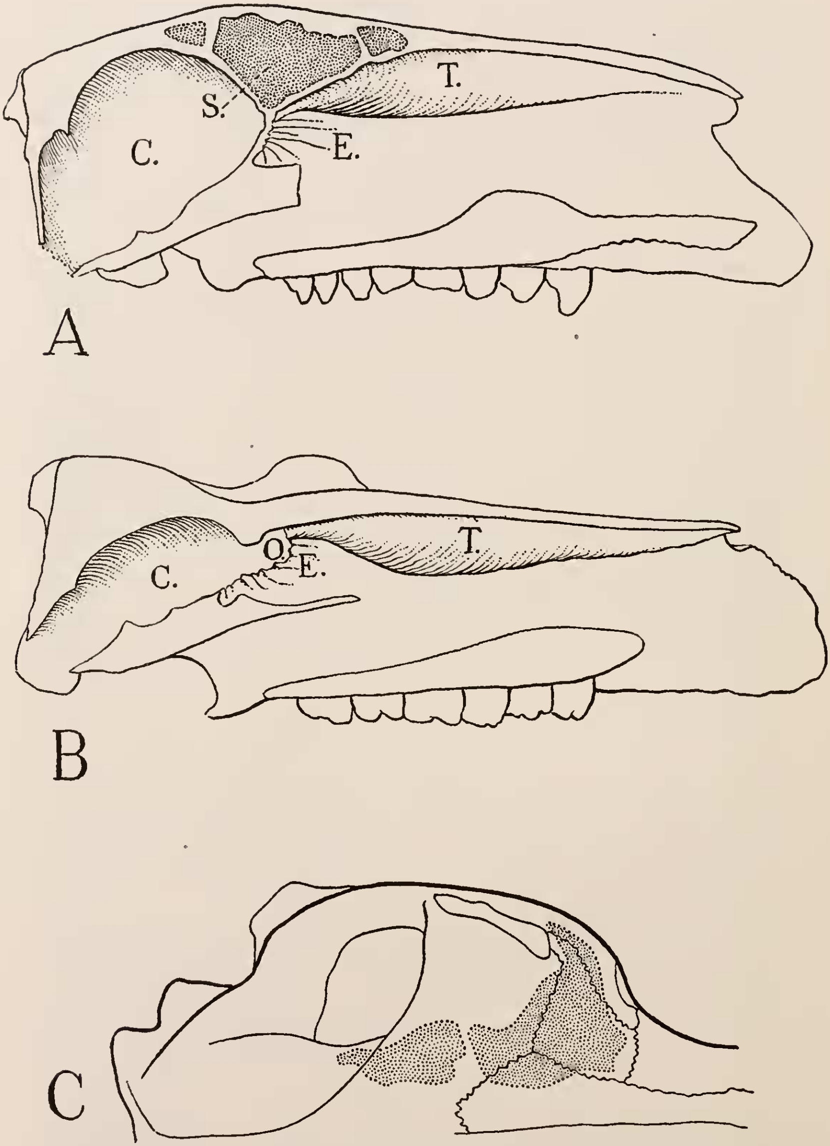


Fig. 5. A: *Choeropsis liberiensis.* Left half of skull. ⅓ nat. size. After Milne Edwards. B, C: *Hippopotamus amphibius.* B: as A, ⅙ nat. size. C: dorsal view of left half of skull, with position of fronto-parietal and fronto-naso-lacrimo-zygomatic sinuses stippled. After Paulli. Reduced.

and figured two compartments (1900, p. 202; our fig. 5 C). One pneumatizes the anterior region of the orbital plate of the frontal, and the lacrimal, zygomatic, nasal and nasoturbinal bones; the other compartment lies in the posterior part of the frontal and the anterior part of the parietal. The latter is seen in *H. amphibius* MCZ Dept. of Mammals no. 6119 which is the left half of a 735 mm.-long skull. This frontal sinus proper begins over the anterior slope of the cerebral chamber very close to the olfactory window, is widest alongside the olfactory bulb chamber, has two diverticula laterad into the posterior region of the orbit roof, and a foreward diverticulum which makes its total length 180 mm. Paulli's specimen seems to have lacked these pockets; still, his repeated "very small" is true also of the sinus in our specimen if it is compared with, e.g., a horse, for in this hippo the frontal sinus extends nowhere nearer to the median plane than 25 mm. Thus it was separated from its opposite not by a septum, but by an unpneumatized region with a minimum breadth of 50 mm.; the region is occupied by rather loose cancellate bone. — As Paulli (loc.cit.) stresses "the extraordinarily small extent of pneumatization in *Hippopotamus*", one is reminded of the absence of sinuses in the aquatic orders of mammals; a relation between non-pneumatization and life in the water is suggested. This, however, cannot be the cause of the difference between *Choeropsis* and *Hippopotamus*, because both lead the same amphibious life. Quite a different explanation of the more extensive pneumatization in the smaller form is indicated by Milne Edwards' two sectioned skulls (our figs. 5 A and B) and his description of their endocranial casts. Comparing the two brain forms, he found that the most striking difference between them is in the olfactory bulbs: "vertical" in *Choeropsis*, in *Hippopotamus* "long" and much more voluminous (loc.cit., p. 52, 53). The bulbi lie along the lower front region of a rounded cerebrum in the short skull of the pigmy, whereas in the long skull of the large form long bulbi continue the oblique axis of the cerebral hemispheres; the MCZ skull shows how their chambers extend upward and come close to the tabula externa of the frontal bone. Another circumstance providing more space for a frontal sinus in the pigmy is its vaulted skull roof; this is flat in the large form, a depression between the huge tubular orbits. In consequence of these internal and dorsal surface differences between the two skulls, the thickness of the frontal bone between cerebrum and olfactory bulbs (as measured in Milne Edwards' pl. IV) is 42 mm. in the 310 mm.-long *Choeropsis* skull, but 32 mm. in the 652 mm.-long *Hippopotamus* skull. Only one-third of the cranial height, this cerebro-olfactory "septum" is not pneumatized in the larger form; one-half of the cranial height in the small form, it is fully pneumatized.

In another order, Carnivora, one finds a similar relation between position of olfactory bulb chambers and size of frontal sinus in the large Felidae described by Hopwood (1947). Hopwood's objects were skulls of the lion and skulls of similar size of two smaller forms, cheetah and leopard. These also are another example of the fact that sinus size can be independent of skull size. "The sinuses of the Cheetah are much greater than those of the Leopard. The largest is the frontal sinus" (Hopwood 1947, p. 369). The leopard agrees with the lion, and with the cat (p. 370). Other differences of the skull interior are "the different extent to which the face is bent down on the basicranial axis (least in the Leopard, greatest in the Cheetah), and the relative volume of the interior of the brain-case (least in the Lion, greatest in the Cheetah)" (p. 373). Hopwood's pl. VI, showing medio-sagitally sectioned skulls of the three forms, and pl. VII which shows their endocranial casts, illustrate these features. They further demonstrate that in the cheetah "the bending down of the face . . . has prevented any real shortening of the olfactory lobe" (the bulb) "and has carried it downward" (p. 374). Whatever the reason, the olfactory bulb chambers lie much deeper within the skull in cheetahs than in lions and leopards. Correspondingly, of two skulls of about equal length shown sectioned in Hopwood's pl. VI, the cheetah specimen has a frontal sinus just double the depth, paramedially, than the leopard specimen.

But Paulli, after his extensive survey (1900, p. 562), claimed to have found that within each order of mammals the extent of pneumatization in the adult is directly proportionate to the size of the animal! Obviously, this is too sweeping a statement. Concerning the order Carnivora, Paulli was mistaken in believing that the frontal bone is never pneumatized in either Viverridae or Mustelidae. Other authors have found the sinus in representatives of both families of small-sized carnivores (Weinert 1925, p. 257, 262; Anthony and Iliesco 1926), including the diminutive weasel (Allen 1882, p. 142; Zuckerkandl 1887, p. 46).

Absence of frontal sinuses in Mustelidae is also maintained by Weinert (1925, p. 257); and he reports the same condition in foxes (p. 259), while according to other authors the structure of the nasal and paranasal cavities of dog, fox and wolf are identical "to the smallest detail" (Zuckerkandl 1887, p. 48).

There are, I believe, two reasons why authors disagree on the presence of frontal sinuses in some Carnivora, all of which normally do have some air cavity within the frontal bone. One reason are the considerable differences between specimens, differences (1.) of skull structure within species such as "the dog", and (2.) of sinus structure within the lifetime of the individual. The second reason for the contradictory statements in the literature is connected with the latter peculiarity of carnivores, and is only a matter of different nomenclature.

In general, turbinals are attached to the anterior and lower surfaces of the ethmoidal chamber walls; in some Carnivora they arise, in addition, from an anterior part of the dorsal surface. Thus the nasal organ with its dorsoposterior extremity can occupy an area which in general is a typical frontal sinus area — and at least in some of the carnivores the nasal organ, during its ontogenetic enlargement, expands into the sinus of the frontal bone. This process is described by Paulli, who studied the heads of 35 dogs of different ages (1900, p. 492, 563, and 3 figures on pl. XXVII: puppy, young dog, adult dog). The frontal sinus is not developed in the new-born, is still wholly empty in the four-week-old, and is gradually entered, through a gradually enlarging foramen, by a turbinal which gradually unfolds in an antero-basal sinus region, and later by the posterior tip of another scroll. In Paulli's diagrams of cross-sectioned skulls of a large and a small dog (figs. 4, 5), *Ursus* (fig. 8) and *Nasua* (fig. 10), one can see that even the invaded compartments of the sinuses remain empty to a large extent. Yet this is the condition frequently described, for example by Allen, as follows: "In the otter, the mink, the weasel, and the bear, the frontal sinuses are occupied by the ectoturbinals" (1882, p. 142); and it is the reason why some authors (e.g., Weinert) prefer to call the frontal bone cavity of some carnivores not a sinus, but a frontal bone niche. Certainly in the anatomy of the adult the communication between the invaded sinus and the nasal cavity is wide, not a narrow foramen; and its contents indeed function as part of the nasal organ. However, no anatomist denies the name sphenoidal sinus to the cavity on the opposite side of the ethmoidal chambers, which in numerous mammals fills with nasal scrolls. Further, besides having the same ontogenetic development, the invaded compartment of the frontal sinus is set off from the adjoining sinus compartments (where such are developed) in the general fashion of sinus partition. In the large dog skull no. 5215 (MCZ Mamm. Dept.) this most anterior compartment is limited posteriorly by a transverse septum projecting into the sinus from the entire periphery of the cavity; this septum frames a transverse window, whose "sill" lies directly anterior to the upper frame of the ethmoidal window. Behind this incomplete partition lies a large empty sinus in this large dog skull, and a smaller one in the pug skull no. 7300. Likewise, in *Viverra civetta*, "the posterior half of the frontal sinus overlies not only the olfactory bulbs but also the anterior part of the cerebral hemispheres" (Anthony and Iliesco 1926, p. 1009). Anthony and Iliesco's fig. 6 shows just such a sinus also in a 110 mm.-long *Meles taxus* skull. It follows that genuine frontal sinuses are a general character of the extant Carnivora fissipedia, large or small.

The more Recent material is compared, the more doubtful one becomes about the importance of general size in pneumatization. The matter might be less obscure if in comparing small with large forms one had distinguished between forms primitively small and dwarfed forms; and among the latter one should distinguish between skulls which are miniatures of the standard size and those in which dwarfism is accompanied by features aberrant, often greatly aberrant, from the norm. It seems reasonable to assume that sinuses expand concomittant with evolutionary size increase but that their extent is not necessarily reduced when a specialized skull is reduced in size. In the pigmy hippo we have seen a case in which a dwarfed skull is even more pneumatized than the giant skull of the nearest relative. On the other hand, the frontal sinuses of large *Canis familiaris* such as the wolfhound are absent in dwarfed *Canis familiaris* if as aberrant as the Pekinese. This difference has been convincingly explained by Weidenreich (1941, p. 430–431). In the Pekinese the braincase is relatively so large that its surface provides an area sufficient for the attachment of the masticatory muscles. In large dogs the cranial surface must be enlarged by sagittal and nuchal crests and braced by postorbital processes, structures which provide space for pneumatization. The braincase, relatively small in large dogs, ends some distance behind eyes and tooth battery; the skull region in front of the anterior pole of the brain, "a special intermediary portion, which is completely missing in dwarf types and consists chiefly of the frontal sinus, joins the maxilla to the brain case" (Weidenreich 1941, p. 339; it is the naturally rounded roof of this region which in the literature is usually described as a domed forehead *due* to sinuses in the frontal bone). Weidenreich found the same contrast in the degree of pneumatization when he compared small with large Felidae, marmosets with Cercopithecidae, the pigmy *Pan paniscus* with *Pan schweinfurthi* — "wherever small types contrast to large ones" (loc. cit.).

As lap-dogs and pigmy chimpanzee can be regarded as dwarfs developed from the larger forms, these cases show that a frontal sinus can be lost, and why. On the other hand, the extant mammals do not and cannot reveal how their frontal sinus originated; as to the why of frontal sinus occurrence, our survey of some extant cases shows that many a special condition remains enigmatic under explanations based on comparative anatomy. These interpretations are mechanical, and they are reasonable. But it should be realized that they do not describe how the present-day condition actually arose. To a paleontologist, at least, it is clear why a possible explanation of frontal sinus occurrence and extent in one group will not explain the condition in another group. Today's conditions are, of course, the outcome of difference phyletic developments. Comparisons of the anatomy of one living mammal with another are not descriptions of evolutionary processes, while frequently the wording of such comparisons implies that they are. One example shall be quoted here, also because it adds descriptions of some more of the various extant conditions to those given above. These remarks on the osteology of living ruminants follow in the Zittel-Woodward textbook (1925, p. 206) the statement that in *Bos* the parietals are pressed into the occipital surface. "With the expansion of the frontals is frequently united a considerable extension of the frontal sinus. The cancellated tissue is replaced by air-cells and the frontal region exhibits a pneumatic condition. In the antelope this peculiar formation of the frontal zone may be traced step by step in its development. While in certain gazelles the frontal bones are still furnished with osseous cancellated tissue . . . in others larger or smaller air cavities are present."

To trace step by step when and how a sinus actually evolved in the frontal zone one must study an ancestral series of mammals — that is, fossil material — in the opinion of the present writer, a paleontologist. The opposite opinion is held by Weinert. His survey of pneumatization in the extant mammals (1926) makes their frontal sinuses features of crucial importance in the study of their evolution. Weinert found one could "trace the ancestral connections in the animal kingdom by investigating their frontal sinuses" (p. 369; e.g., man can have evolved only from "sinus-bearing anthropoids", p. 385).

3. Some extinct cases

Survey. Paleontologists, unfortunately, have paid little attention to the occurrence or absence of pneumatization in Tertiary mammals. Frontal sinuses of many Pleistocene mammals are mentioned in the literature; but conditions in the Pleistocene will hardly teach more about sinus evolution than present-day conditions. While I have not made a systematic hunt for references to skull pneumatization, I have taken notes from the literature ever since I studied the phenomenon in Reptilia (1938). Mr. Bryan Patterson of the Chicago Natural History Museum, who has just now under way studies which will incidentally fill some of the gaps in our knowledge of ancient frontal sinuses, has most generously kept me informed on his findings and has given permission to use in the present paper his unpublished discoveries; he has, in addition, supplied me with references I had not come across myself. I realize that I must have overlooked some (or many) more references in literature. Nevertheless I believe that paranasal sinuses have been mentioned or described in only one or very few Tertiary genera from only some of the orders of mammals; even less are figured. Almost all the data reported below, culled from the literature or seen in specimens, are based on what chance breaks have revealed. With the data so poor, a survey of what is known seemed of little use in our quest after frontal sinus origin. The review was undertaken for negative reasons rather than in the expectancy of positive results. Read in connection with my study of the Equidae, some interpretations in the paleontological literature seemed open to doubt. I could not agree that everything described as a frontal sinus really was one. For example, frontal sinuses in fossil Equidae are twice mentioned in the literature; actually, the cavity in question is the olfactory bulb chamber in one case (see p. 442), the cerebral chamber in the other case (p. 484). Interpretation of cavities sometimes appears to be founded more on the author's awareness of conditions in Recent skulls than on what is seen in the fossil. Study of non-equid early Tertiary specimens had to supplement the study of the controversial literature. Positive results as to the main theme of the present paper were incidentally obtained; e.g., relatively late acquisition of a frontal sinus was not a phenomenon particular to the Equidae.

Haplolambda. Our review begins with a postscript. As the present paper was being finished, a letter from Mr. Patterson reported his discovery of a frontal sinus in *Haplolambda*, Upper Paleocene pantodont. Mr. Patterson sent me a sketch showing the cranium sectioned in the midsagittal plane. Almost half of the section consists of the enormously thick cranial roof. The sinus invades only an anterior portion of the lower half of the roof. It lies above the large olfactory bulb chamber and has a posterad diverticle over the anterior slope of the cerebral chamber. In another *Haplolambda* specimen Mr. Patterson found this sinus continued forward in the frontal bone at least as far as the postorbital process, which is invaded by the sinus. This is the oldest case of pneumatization we know of. According to Mr. Patterson's estimate, the skull to which the sectioned cranium belongs was ± 380 mm. long. The animal had been a giant among the Paleocene mammals which were, in general, small.

Dorudontidae. The spaces quoted as cetacean frontal sinuses since Stromer's (1903, 1908) description of Middle Eocene endocasts are, in my opinion, not paranasal but nasal cavities. The surface of the casts is fluted as are only casts of cavities containing turbinals. Actually, Stromer himself described the "sinus frontales" as "mit Nasenmuscheln gefüllte Hohlräume" (1908, p. 118). Similarly, Kellogg writes (1936, p. 200): "The longitudinal grooves on the dorsal surface of the frontal sinus mark the position of the inner chambers which are enclosed by the scroll-like ethmoturbinals." It is true that turbinals can project into the frontal sinus (in macrosmatic mammals: Carnivora, see p. 439) which otherwise, however, remains an empty space. A cavity "filled with nasal conchae", and anterior to the olfactory bulbs at that, is not a sinus.

One *Dorudon* endocast specimen, however, includes casts of paired lateral cavities whose surface is smooth (Stromer 1903, pl. X, fig. 2 and pl. XI, figs. 2, 3, "f"). Their position is immediately anterior to the orbit, their anterior end in the plane of the infraorbital foramen; medially they communicate with the nasal cavity. Stromer thought these cavities probably were nasoturbinal, but found their projection laterad, into the upper posterior part of the maxillary, "quite unexplainable" (1903, p. 74). Here was no doubt a pair of pneumatic spaces, rightly interpreted by Kellogg (1936, p. 215) as maxillary sinuses. Apparently skull pneumatization in the large Eocene whale was comparable to, yet less than that in the tiniest of living ungulates, *Tragulus,* whose only sinus lies in the maxillary, lacrimal and zygomatic bones (Paulli 1900, p. 210, 246). For posteriorly in the Eocene archaeocet skull, notwithstanding the presence of a sagittal crest and conspicuous thickness of the roof bones, there was no pneumatization. The parietal, which roofs the brain, is shown in the intertemporal region anterior to the cerebrum in Kellogg's cross section of a *Zygorhiza* skull (1936, fig. 31 b). Excepting the canals for the ophthalmic nerves, there is no cavity in the 74 mm.-high and similarly broad bone above the olfactory peduncles. The frontal bone mass which more anteriorly overlies the long peduncles is described by Stromer as "innen fein spongiös" (1908, p. 116; pl. V, fig. 13). Cetaceans presumably never developed a frontal sinus. The fate of the maxillary sinus is not known except that today it has disappeared; Stromer searched in vain for a similar cavity in *Balaenoptera* (and in *Phoca;* 1903, p. 74).

Canidae. In *Pseudocynodictis,* whose described Middle Oligocene skulls are 89-92 mm. long, "there are no frontal sinuses" (Scott and Jepsen 1936, p. 84; also Scott 1898 b, p. 370). *P. gregarius* AMNH 1408 distinctly shows that there is no cavity whatever within the frontal bone over and forward from the anterior poles of the cerebral hemispheres. Great significance has been attributed to this condition. Scott, discussing the probable relationships of *Pseudocynodictis* (then called *Cynodictis*) with other Canidae, regarded as "certainly a suggestive fact that *Cynodictis,* like the foxes, is devoid of any frontal sinus, while all the other American genera, from *Daphoenus* onward, have well-marked sinuses, as the wolves" (1898 b, p. 404; cf. our p. 438). In the 1936, revised description of *Pseudocynodictis,* the absence of frontal sinuses still appeared important enough to be noted as "a difference from *Daphoenus* which, in this respect at least, agrees with

Huxley's thoöid division of the Canidae, while *Pseudocynodictis* agrees with the alopecids, or foxes" (p. 84).

Daphoenus, a contemporary of *Pseudocynodictus* with skulls 1½ times as long, actually may not have had the "large frontal sinuses" recorded by Scott in 1898 (b, p. 332, 410). According to Scott and Jepsen 1936 (p. 58), "None of the available skulls is so broken as to expose the sinuses, but the convexities of the forehead seem to indicate their presence, though those convexities are not a sure proof of the existence of frontal sinuses, as *Urocyon* demonstrates" (a fox). At the Chicago Natural History Museum I have seen the endocast specimen on which Moodie based a description and figure of the frontal sinuses in *Daphoenus* (1916, p. 142-143, fig. 3). Moodie labelled "sinus frontales" three pairs of low and narrow longitudinal endocasts extending forward from the dorso-anterior end of the cerebral chamber cast. The middle pair, for example, is 19 mm. long, and the greatest breadth of each member — in the middle of its length — is 4 mm. Obviously, these casts were molded in narrow turbinal scrolls. A similarly low, channeled endocast is seen in this position, i.e. reaching back over the olfactory bulb chamber, in the indeterminable Oligocene canid endocast specimen AMNH 8767. Thus in such larger Middle Oligocene Canidae as *Daphoenus*, the nasal apparatus extended dorso-posterad as in Recent dogs, and one can reasonably assume that the low space into which the extensions protruded was pre-formed as a frontal sinus. Moodie believed that *Daphoenus* had a large sinus, "singularly like the frontal sinus of the modern dog", because he assumed that "the posterior superior portion of the cavities has been lost". Actually, however, the specimen is a complete endocast.

Large frontal sinuses above the braincase were present in later and larger Canidae, such as a Miocene *Amphicyon* (Patterson, personal communication) and a Pliocene *Pliogulo* (a form with a 230 mm.-long skull — White 1941, p. 67).

Merycoidodontidae. I have noted (1948, p. 60-61) that *Merycoidodon* and other Middle Oligocene artiodactyls had, like the contemporary *Mesohippus*, the olfactory bulbs in a high position anterior to the cerebrum. Scott has shown this condition in still another White River artiodactyl, *Stibarus* (1940, pl. XXXVI, fig. 2). The specimen graphically illustrates the relation of dorsal frontal sinuses to brain shape. It is a muzzle lacking the bones posteriorly so that there are exposed the natural endocasts of the anterior cerebral, the ethmoidal, and some of the turbinate cavities. In the side view, the dorsal surface of these casts and the preserved nasal bone form practically one line;

there was no room in the roof part of the frontals in which a sinus could have developed.

In *Merycoidodon* (*Oreodon*), Moodie (1922, p. 366-367) found latero-dorsal "Sacculations of the sinus maxillaris superior", and they are shown in his fig. 21, a dorsal view of his specimen. These pneumatic compartments are indeed not what is usually termed maxillary sinus, but a pneumatic area which in all studies of adult *Equus, Bos,* etc. is described with the frontal sinus, with which it is confluent. The ontogenetic stories reported p. 419 suggest that this anterior space develops before the cranial sinus. It is the pneumatization of the orbit walls. Many *Merycoidodon* specimens show its endocasts; MCZ 17397 shows them particularly well. There were lateral sets of cavities, or compartments of a sinus. This sinus was in great part in the frontal bone, namely, in the pars orbitalis ossis frontalis. The postero-lateral edge of the most posterior compartment protrudes somewhat into the insertion of the post-orbital bar; in contrast to *Mesohippus,* this bar is in *Merycoidodon* a voluminous structure proximally, and with its more slender distal part it closes the orbit which in *Mesohippus* is still open posteriorly. Compared with the slim skull of *Mesohippus,* the thick orbit roof and zygomatic process appear like "superstructures" in the broad, "piglike" *Merycoidodon* skull. Their pneumatization, incidentally, is similar even in details to that in the living *Capreolus* (Paulli 1900, fig. 30-31, p. 220-221).

A frontal sinus proper, in the middle roof region, was not developed in *Merycoidodon.* Moodie believed that in his specimen "frontal sinuses" had been present and that "we have the bulbs exposed in *Oredon gracilis* because the sinuses have been broken away." However, nothing is broken away from the specimen studied by Moodie — except bone, of course —. Mr. Patterson has kindly studied with me this specimen, and I have seen many other endocasts as well as many broken and sectioned skulls of *Merycoidodon;* the MCZ alone has seven skulls of *M. gracilis* and *affinis* broken across the ethmoidal or the cerebral chambers. There is never a sinus in the roof of either of these chambers; always cancellate bone tissue occupies the low space between inner and outer plates of the roof portion of the frontal bone. Occasionally spongiosa cells combine to form a larger cell — whose endocast, however, can be seen to be criss-crossed with bone laminae. It must have been such cell-clusters of which Moodie wrote: "A group of small cavities, just anterior to the brain are, doubtless, all divisions of the frontal sinus" (1922, p. 140), in his description of an endocast he believed to be *Merycochoerus* (1916, p. 135-141, fig. 1-4; 1922, fig. 17). However, Mr. Patterson assured me that no such matrix, no such natural endocasts are found in the Miocene and that Moodie's

"*Merycochoerus*" specimen appears to be another White River Oligocene *Merycoidodon*, probably *M. culbertsoni.*

In one *Merycoidodon* only have I seen a cavity large enough to be regarded as an incipient frontal sinus proper. In *M. gracilis* MCZ 16272 the frontal bone is chipped off dorsally in the anterior brain region, but was left in situ laterally. Here is seen the endocast of a small cavity which is posterior to the cavity in the orbit roof and separated from it by a bone wall. In the dorsal view which this specimen exhibits, the cavity has the shape of a triangle; the 4 mm.-long, longitudinal "base" is lateral, in the outer cranial wall at the postorbital constriction; the 4 mm.-distant "apex" points mediad between cerebral and olfactory chambers, whose walls constitute the sides of the triangle. Thus the incipient frontal sinus proper of the Merycoidodontidae was in a position corresponding to that of the basal pockets of the *Equus* frontal sinus.

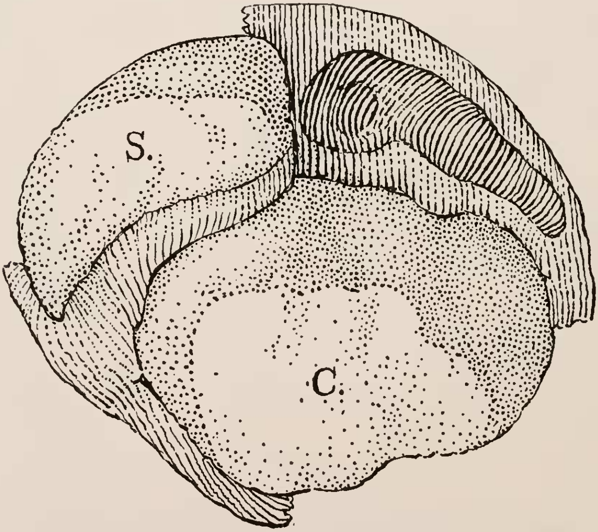


Fig. 6. *Eporeodon socialis* (M.C.Z. 5279). This anterior view of the posterior skull fragment shows the fragmentary frontal bones enclosing the natural endocasts (stippled) of the cerebral cavity and the right frontal sinus; the endocast of the left sinus was removed so that its posterior wall is seen. 2 x nat. size.

A radically changed condition was found in the Upper Oligocene direct descendant of *Merycoidodon, Eporeodon.* MCZ 5279 is a skull of the robust Upper Brulé *E. socialis,* in length (about 230 mm.) and general bulk about double the size of *M. gracilis* skulls. It is broken in two along a transverse plane closely behind the anterior end of the cerebrum. Atop the frontal part of each cerebral hemisphere lies the endocast of a considerable frontal sinus (fig. 6). Both these endocasts can be easily detached, whereupon the typical smooth sinus walls are revealed. These sinuses were developed in an area of the frontal which in *Merycoidodon* was a low layer of cancellate bone.

The anterior surface of the *Eporeodon* frontal sinus has the shape of a drawn-out drop. Its proximal part, horizontal, is 8 mm. high. It tapers out latero-basad, where its curved end envelops laterally the upper part of the cerebral cavity; this lateral end region alone was the frontal sinus in the ancestral genus. The total anterior breadth of each sinus is 17 mm. The antero-posterior length is also 17 mm. The lateral walls converge, and the posterior end of each sinus is a circular posterad groove with a 3 mm.-diameter. Its position is noteworthy with regard to the relation of sinuses to superstructures. The sinus ends, inside the frontal bone, where on the outside the medio-sagittal crest splits into the pair of temporal ridges. The area of the end-groove is marked on the dorsal skull surface by the angle which the posterior end of the temporal ridge forms with the median suture of the frontals. The median septum sinuum frontalium increases considerably in breadth as it approaches the end of the sinus — and the external crests.

When one compares with this *Eporeodon* specimen corresponding cross sections of *Merycoidodon* skulls, the impression is that something has lifted the tabula externa ossis frontalis up and away from the braincase. Comparison of intact skulls of ancestor and descendant gives the explanation. The *M. gracilis* cranium roof is practically level; but in *E. socialis* the two sides rise toward the midline, which projects upward in a voluminous ridge — the sagittal crest, noted as sharply prominent and 57 mm. long even in a smaller individual of *E. socialis* (skull length 199 mm.; Thorpe 1931 a, p. 12, p. 19). The supra-cerebral sinuses, acquired in *Eporeodon*, anteriorly join, beyond incomplete septa, the lateral supra-orbital sinuses, acquired earlier; and medially there is now a pair of sinus compartments overlying the olfactory bulb chambers. These compartments are small in dorsal view, and they are presumably not deep; for in *Eporeodon* the cerebral "superior surface slopes gradually forward, not after the abrupt manner of the slope in the horse, but rather more like that of the pig" (Thorpe 1931b, p. 194).

It should perhaps be noted that the condition here described of *Eporeodon* is a supplement to Thorpe's classic on the Merycoidodontidae. Its chapter "Sinus paranasales" only repeats Moodie's descriptions, because Thorpe believed that "the general pattern is the same in all of them" (viz., the mercoidodont genera; 1937, p. 269).

Protoceras. Together with *Eporeodon socialis* lived *Protoceras,* whose males were the most-horned of ruminants. From skulls similar to large *Eporeodon* skulls in length (250 mm.) there projected, besides a thick sagittal crest, five pairs of bony protuberances. To judge from the literature, none of the paired superstructures was pneumatized. Two of them were enlargements of the frontal bones. Marsh described the frontals of the male *Protoceras* as "massive bones" (1897, p. 169). Pneumatization of a small degree was discovered by Scott. The parietal crest is "cancellous internally and encloses a small sinus", and besides this one "There is a small frontal sinus" (1940, p. 571, 573).

Archaeotherium. In this huge, pig-like Middle Oligocene artiodactyl, on the other hand, Scott found large sinuses — "giving the convex shape of the forehead" — when he studied three particularly large skulls, 746–803 mm. long (1898 a, p. 280). In *Archaeotherium* generally, "sinuses extend through the whole length of the parietals and even invade the supraoccipital. . . . The frontal sinuses are large and seem to communicate with the parietals" (1940, p. 384). "The great frontal and parietal sinuses overlie the whole cerebral chamber" (1898 a, p. 287; 1940, p. 388–389). Indeed, as in pigs, they extend back over the entire brain; and their height equals that of the brain chamber in the medially sectioned cranium Princeton University no. 10908. A transverse break in another Princeton specimen (no. 12532) shows the oval of the sectioned cerebral chamber surmounted by another hollow structure, which is triangular in the section: a large, fully pneumatized sagittal crest.

Edentata. Certainly because it was G. G. Simpson who collected and studied South American early mammals, frontal sinuses are recorded from three of the orders represented in the Casamayoran, the first half of the Eocene in that continent — Edentata, Astropotheria, and Notoungulata. Of *Utaetus,* a Casamayoran dasypodid, Simpson reports that "as in other armadillos the anterior parts of the frontals contain extensive sinuses" (1948, p. 83).

Astropotheria. In a skull of the oldest of Astropotheria, *Trigonostylops,* Simpson found already present that characteristic of its descendants, a domed forehead — "the frontals themselves being markedly convex and inflated by large sinuses in at least their posterior part, which is all that is preserved of them on the skull roof" (1933 a,

p. 9). This skull is about 220 mm. long in Simpson's reconstruction (fig. 1). Its snout is not preserved. This is an unfortunate circumstance, because the muzzle shape of later Astropotheria skulls suggests that these heads had a proboscis; among Recent mammals, this is an element correlated with the highest degree of pneumatization. In the 590 mm.-long skull of the Lower Miocene *Astropotherium* described by Scott (1928, 1937), "The great dome of the forehead, caused by hypertrophied frontal sinuses" is a most conspicuous feature; "fractured specimens show that this highly characteristic dome is filled with a complicated system of communicating cells" (1937, p. 315, 317). Mr. Patterson found an enormous main cavity with irregular, incomplete septa.

Toxodonta. The four notoungulate genera whose frontal sinuses have been described are from four different stages of the Tertiary but unfortunately do not form an ancestral series. They represent four different families — which, however, all belong to the suborder Toxodonta (Simpson 1945, p. 126–128). The Upper Eocene *Rhyphodon* had a frontal sinus unusually large for a relatively small mammal of that period. The anterior region of its brain, too, has an unusual configuration. Simpson, comparing the brain of *Rhyphodon* (skull length about 230 mm.) with those of two Lower Eocene mammals, *Phenacodus* (skull length 237 mm.) and *Notostylops* (skull length about 115 mm.), found the brain portions arranged in similar fashion, "except that the olfactory bulbs are bent downward (they are overlain by large frontal sinuses absent in the other genera here described)" (1933b, p. 15). Skull superstructures — sagittal and lambdoid crests — were present in both these other genera; but inside the skull of both *Phenacodus* and *Notostylops,* the olfactory bulbs extend straightly forward anterior to the cerebrum and thus are roofed directly by the skull roof (see Simpson's fig. 3C, 1932, which shows the endocast in a sideview of the skull of *Notostylops.*) The bulbi of *Rhyphodon,* on the other hand, are peculiarly drawn out and down; their dorsal surface is in the same horizontal plane as the fissura rhinalis of the cerebrum, and half the cerebrum lies above this level. The relation between this brain form and the occurrence of a sinus above the bulbi seems, to me at least, obvious.

The Miocene *Homalodotherium* also has a large frontal sinus. The sinus is likewise present in *Rhynchippus* (Oligocene) and *Nesodon* (Miocene), but in these genera "it is smaller and situated more anteriorly" (Patterson 1937, p. 290). Corresponding are, I believe, the main differences between the brains of *Homalodotherium* and *Rhynchippus,* as noted by Patterson loc. cit.; in *H.*, the form with the larger sinus, "the olfactory bulbs are greatly depressed . . . the anterior third of the cerebrum is greatly depressed".

It seems to me that the smallness and anterior situation of the frontal sinus in the Miocene *Nesodon* are also related to the position in the skull of the anterior brain regions — which in this case is obviously due to a peculiarity of the skull. "The basifacial axis is bent down on the basicranial . . . the cerebrum is inclined upward" (Patterson 1937, p. 282). Patterson's side view of the *Nesodon* brain (fig. 77) shows that here the bend is more anterior than in the cheetah (see p.438), for in *Nesodon* the olfactory bulbs rise upward towards the skull roof. Their dorso-anterior vault is only 10 mm. below the dorsal vault of the cerebrum. Their position in the skull is so high that their ventro-anterior tip is on a level 54 mm. above the pituitary region of the brain stem. Such a brain directly suggests that in its capsule there cannot have been much of a frontal sinus (but there should have been much room for a sphenoidal sinus).

A large frontal sinus has recently been found in an early Oligocene notoungulate by Mr. Patterson. The specimen is an about 400 mm.-long skull of *Leontinia*. The sinus is 77 mm. long, and 25 mm. deep just off the midline. The case possibly parallels that of the elephant (p.435), as in *Leontinia* "a high position of the nostril opening suggests the presence of an expanded muzzle or proboscis of some sort" (Romer 1945, p. 396).

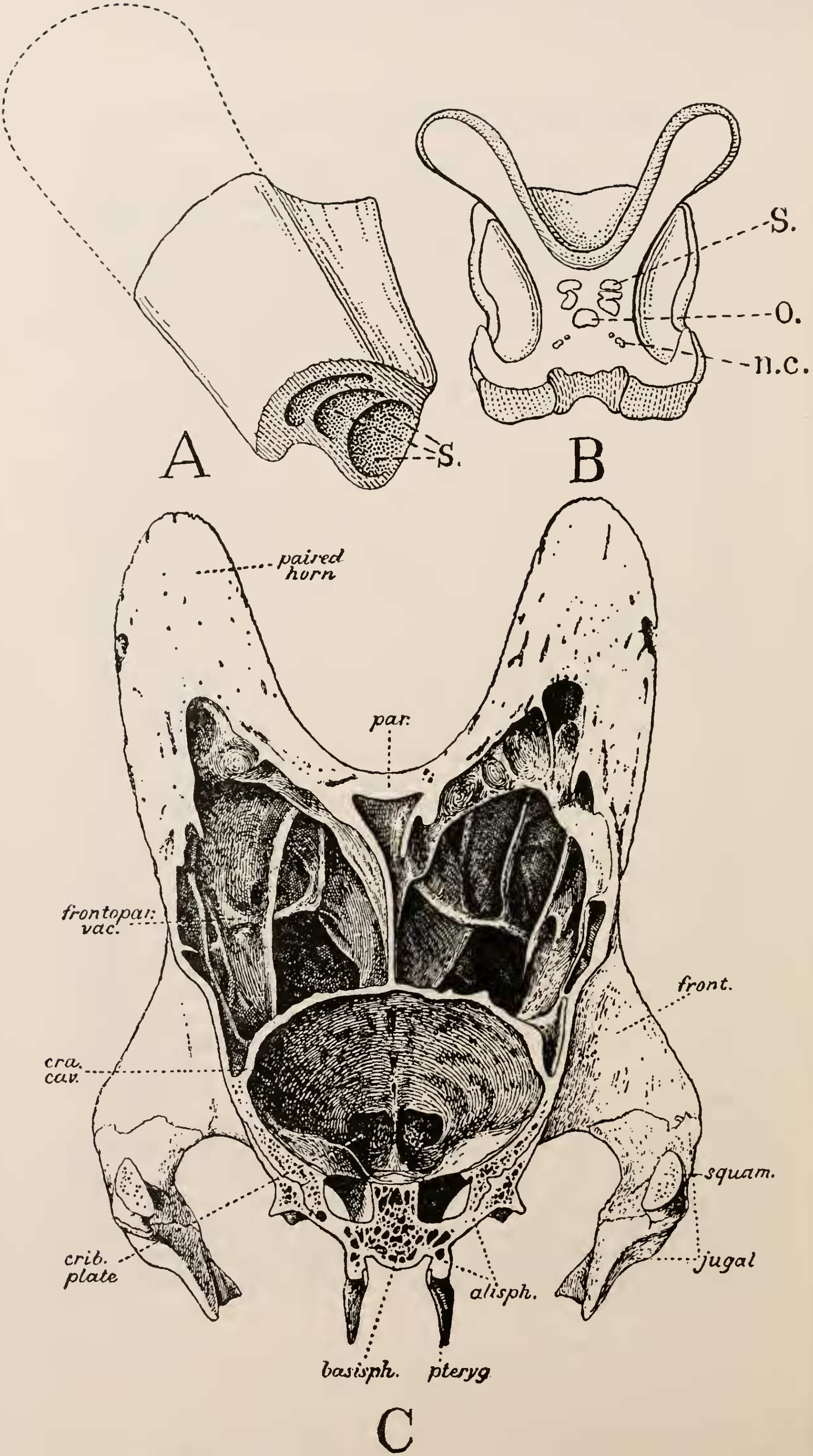
Uintatherium. The cavities in the skull of the Dinocerata have, it seems, not been studied since the 1880s — at that time, however, by the then greatest paleontologists. To judge from the descriptions, there was very little pneumatization of the frontal bone in that archaic group of ungulates. Yet the Middle Eocene American genus, *Uintatherium*, was as large as a Recent African rhinoceros; and its skulls, 760–870 mm. long, had developed superstructures to the extreme of three pairs of horns plus a crest around the posterior and lateral margins of the cranium.

The smallest of the horns are swellings of the nasal bones, which are "thick and massive" (Marsh 1886, p. 12).

A large cone rises from each maxillary bone. "The maxillaries are massive . . . The cones are solid except at the base, which is usually perforated for the fang of the canine tusk" (Marsh 1876 a, p. 164). When Marsh later, in his Dinocerata monograph (1886), described those upper canines, he wrote that in dinoceras "the root extends upward into the base of the maxillary protuberance, or horn-core" (p. 43), whereas in tinoceras "the root, instead of being inserted in the base of the maxillary core, starts well back of it" (p. 46). However, Marsh's "Dinoceras" and "Tinoceras" skulls belong to the same genus, viz., *Uintatherium.* The canine socket may in some individuals have projected into the cavity in the horn base (as do the molar sockets into the maxillary sinus of, e.g., horses), but that cavity is never identical with the canine socket. Its lower regions are seen in Marsh's four horizontally sectioned skulls of "Dinoceras" as well as "Tinoceras" (figs. 30–33: "cavity behind base of canine tusk"). Also in the "Tinoceras" skull YPM 11500 this maxillary sinus is separate from the canine socket. This sinus invaded the horn to a modest degree. For example, the maxillary horn YMP 1534 is 250 mm. long, and the endocast of a sinus seen in its base seems to have been hardly longer than the 25 mm. laid open in the specimen. The horn base, along which the horn broke from the skull, measures 130 mm. across, but the sinus in its center only 66 mm. Two smaller compartments lie along the medial side of this proximal surface of the horn. Among the "striking peculiarities" of a "Tinoceras ingens" skull Marsh mentions that the maxillary protuberances are "greatly excavated within, and below, as shown in fig. 191" (1886, p. 215); but even this horn has only one-fourth of its length pneumatized.

The largest horns of the uintatheres and the wide crest are formed by the parietal bones. Nevertheless, "These bones are thick and massive, but like the frontals are lightened somewhat by air cavities" (Marsh 1886, p. 18). Some pneumatization also of the temporal bone is reported in Marsh's '76 paper; "There are small air cells in the wall of the temporal fossa, both in the squamosal and parietals" (1876 a, p. 164). Whatever there was of cranial pneumatization must indeed have been restricted to latero-dorsal areas. No pneumatic spaces except the maxillary one are seen in Marsh's horizontally sectioned Dinocerata skulls (1886, fig. 30–33), nor in the median skull sections (ibid., figs. 34, 178). The latter figures show how thick was the massive roof of the small brain chamber. Osborn cites among characters shared by uintatheres and elephants "extensive air cavities in the skull" (1881, p. 26); according to his description of the *Uintatherium* skull (p. 43), however, the sinuses he saw are "in the sphenoidal and ethmoidal regions . . . The protuberances are solid above, but hollow at their bases."

The hollow in the parietal horn of the "Tinoceras ingens" mentioned above occupies only one-thirteenth of the length, according to Marsh's fig. 192 (1886) which shows this horn in side view. Among Cope's uintathere material was a fragment of a parietal horn in whose anterior aspect the base is seen to contain "three sinuses" (Cope 1884, p. 57 and pl. XXXIX; our fig. 7A). The "cavities in the cranial walls" of Marsh's cross-sectioned uintathere skull (1886, fig. 35; our fig. 7B)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are similarly subdivided. On the left side three, on the right side two compartments form a sinus, dorsal and lateral to the chamber which lodged the olfactory bulbs, in the otherwise massive frontal bone. These sinuses must have been continuous with the pockets in the parietal horn bases. Uintatheres thus appear to have had a lateral pair of narrow, tunnel-like, longitudinally (and perhaps also otherwise) subdivided fronto-parietal sinuses extending back from the nasal cavity, over the olfactory bulb chambers, to the base of each parietal horn.

It will be noted that none of the long bones of the Dinocerata has a medullary cavity. The inner structure of humerus and femur is described as "somewhat cancellated" (Marsh 1886, p. 91, 141), the distal long bones are "nearly, or quite solid" (ibid. p. 96, 142). This condition illustrates a general tendency to stoutness and heaviness of the skeleton in the uintatheres, a phenomenon which offers one possible explanation of frontal sinuses much smaller than in comparable living forms.

There is, of course, no living form similar to the uintatheres; but some comparison is possible between the uintathere skull and, for example, that of the giraffe, whose interior structure happens to be particularly well figured, by Ridewood (1904). *Camelopardalis* skulls are not quite as enormous as *Uintatherium* skulls, but they are very large (occipital condyle to premaxillary tip 650 mm. in three specimens I measured; *Uintatherium:* 760 mm.), and they do not have three horn pairs, but a pair of fronto-parietal horns plus a median frontal horn. In fig. 7C one is looking forwards into a giraffe skull obliquely sectioned down the front part of the paired horns. This section includes the summit of the fronto-parietal sinus, but not that of the horns; these are hollowed out for about one-third of their length. The section plane is more posterior than that of *Uintatherium;* it crosses not the olfactory but the cerebral chamber. The figure shows, beyond the anterad sloping roof of the cerebral chamber, the ethmoidal windows, and beyond these the cribriform plates: olfactory chambers not anterior, but baso-anterior to the cerebrum. In this respect *Camelopardalis* is as similar to *Equus* as *Uintatherium* to *Hyracotherium*. As regards the sinuses, the figure speaks for itself. Compared with those of

Fig. 7. A: *Uintatherium* (*Loxolophodon cornutum*). Fragment of right posterior horn, anterior view. ⅓ nat. size. After Cope. B: *Uintatherium* (*Dinoceras mirabile*). Proximal side of skull sectioned across olfactory chambers. ⅛ nat. size. After Marsh. C: *Camelopardalis* sp. This posterior view of a skull cut obliquely across the front part of the paired horns shows, below the frontal sinuses (fronto-parietal vacuities), the anterior part of the cerebral chambers (cranial cavities), their anterior limit: the ethmoidal windows, and anterior to these the olfactory chambers, with their anterior wall: the cribriform plate. 2/7 nat. size. After Ridewood.

Uintatherium, the frontal sinuses of the adult giraffe are enormous. They extend forward to below the median horn, and laterally they hollow out completely the postorbital bars (Ridewood 1904, fig. 7).

Arsinoitherium. Pneumatized horn cores are known in one genus of early Tertiary mammals. The only known representative of the subungulate order Embrithopoda, the huge *Arsinoitherium* of the Lower Oligocene, had the tabula externa lifted up on no less than two-thirds of the skull roof by the formation of two horn pairs — or, rather, a set of four horns. The members of each pair are fused medially and the two pairs are fused at their bases. The posterior, frontal bone horns of *A. zitteli* are 327–400 mm. long. The anterior pair, formed partly by the frontals, mostly by the nasals, sweep upward and forward beyond the limits of the skull proper. They are structures with lengths of 640–1094 mm. and a width across of their combined bases, stretching all across the skull, of 168–245 mm. (Andrews 1906, p. 69). "The great anterior horns consist of comparatively thin bony walls which are strengthened by a complex system of buttresses . . . The central portion is occupied by an enormous sinus, the walls . . . 0.5 to 1 cm thick in the adult, and much less in the young. The sinus occupies the bodies of the nasals and frontals and in the latter extends into the small supraorbital horns. Furthermore, it extends back into the parietal, and in the old animal even into the base of the lateral prominences of the lambdoidal crest. In the cranial region the sinus is more or less completely divided into right and left half by a median septum occupying the position of the suture between the parietals. Here the lower table of bone forming the actual wall of the braincase is very thin, while the upper table is greatly thickened". Although not accompanied by an illustration this description, more detailed in the original (Andrews 1906, p. 9), is a convincing record of genuine and extensive frontal sinuses.

There were present in *Arsinoitherium* not only the two obvious factors known to induce pneumatization, a giant skull (length to 800 mm.) and superstructures, but also a third factor contributed to the discrepancy between inner and outer plates of the frontal bone. The frontal region of the *A.* brain is so "prominent and rounded" (Andrews, p. 15) that its profile arches upward from the olfactory bulbs — a progressive feature as uncommon in the early Oligocene as are the hypsodont molars of this form. Measuring Andrews' side views of the *A. zitteli* type (pl. I) and its endocranial cast (text-fig. 5C), one finds that the posterior border of the posterior horns is in the same transverse plane as the anterior end of that part of the cerebrum whose dorsal surface is horizontal; that is, the tabula externa slopes upward just where the tabula interna is inclined downward as it follows the slope of the anterior cerebral surface.

Titanotheres. A discussion of the titanotheres takes us back to the order with whose most common living representative this paper started — the Perissodactyla. Titanotheres, much like contemporary equoids in the early Eocene, became extinct when horses were in the beginning of the *Mesohippus* phase. In America they died out during the early Oligocene, when the Embrithopoda became extinct in Africa; as in that order, the last of the titanotheres were giant forms with paired superstructures on their large heads. Perhaps only a student of pneumatization can quite understand why the horns of the Oligocene titanotheres are referred to as "the so-called horns", "the horns, to call them so", etc. Of course a horn is, to quote Webster, "2. Any natural projection or excrescence from an animal, resembling or suggestive of a horn". Paleontologists must have too much in mind Webster's no. 1 definition, the hollow horn of Recent Cavicornia — and titanothere horns were practically solid, as were those of the uintatheres in a still earlier period of mammal history. Titanotheres (in contrast to uintatheres) are represented in American collections by a vast number of specimens. However, as far as I know, in a century of literature on the titanotheres only four authors have noticed pneumatic spaces in the skull, mentioning them incidentally. Those brief references to titanothere sinuses are confusing. Study of certain Upper Eocene and Lower Oligocene specimens showed conditions which appear to be different from those in all other mammals whose pneumatization is on record. When looking over the many hundred figures of titanothere skulls in Osborn's monograph (1929), one gets the impression that many incomplete specimens display breaks appropriate for sinus studies; but in almost all originals which I have examined the inner structure is hidden under a plaster coat. A study of pneumatization in titanotheres by means of serially sectioned skulls from the different groups is necessary to trace the whole, doubtlessly interesting story of frontal sinus evolution in the titanotheres — but that is beyond the scope of the present survey. So is likewise, I feel, the detailed account given below of the knowledge now at hand. However, the case of the titanotheres is one which adds considerably to the problems of frontal sinus evolution. This is by no means apparent from the previously published, scattered data. These call for correction and amplification.

Marsh (1876 b, p. 335) described the horns of *Menodus ingens* as formed by the maxillaries and containing "large air cavities in the base". Actually, the horns are expansions of the nasal bones. The (lost) type specimen of *Megacerops coloradensis* Leidy consisted of the nasals with the horns, and breaks in many directions gave access to views of the internal structure. Leidy (1873, p. 239) found that "The nasals and contiguous bones are of great thickness, and as solid as those generally in the living Sirenians"; the horns "are large, dense, conical knobs".

Cope, too, described a horn as "a large osseous tuberosity, which consists of a mass of bone, . . . its base . . . not excavated by the anterior part of the frontal sinus" (1874, p. 491–492). This horn belonged to Cope's genus Symborodon, whose species Osborn (1929) has distributed to *Menodus* and *Brontotherium*. Cope's description of the general characters of the genus suggests considerable pneumatization of the skull proper. He calls "the large sinus common to the genus" a "huge cavity" (p. 481–482). This is described as a chamber on each side between the side walls of the long nasal fossa and the lateral skull walls. He makes two seemingly contradictory statements about the posterior topography of these sinuses; they lie in front of the olfactory bulbs (p. 482), they extend above and behind them (same page).

The sinuses along the nasal channel are not mentioned elsewhere in the literature, but Scott (1941), in his summary of the characters of the American Oligocene forms, wrote: "A system of numerous small communicating sinuses was developed around the brain-case, lightening the skull without loss of strength" (p. 874). In the detailed anatomy, however, Scott states that the frontals, the largest elements of the skull, "like the parietals, are very thick because of the cancellous bone, with which they are filled" (p. 884).

The fourth record of titanothere skull pneumatization I found in the literature is the only one showing sinuses in figures — in fact it consists mainly of fig. 254 in Osborn's monograph on the titanotheres (1929). Here are shown longitudinally and transversely sectioned skulls of genera far older than those in which frontal sinuses have been mentioned by Cope, Marsh and Scott. Besides pointing out the sinuses in the legend to fig. 254, Osborn has only occasionally mentioned the presence of sinuses in the figured Eocene titanotheres in the text of his monograph; I found no reference to the sinuses of Oligocene forms. The available data on pneumatization in the three figured Eocene genera will, therefore, be described here (I–III) and followed with my findings in some Oligocene specimens (IV).

I. The Middle Eocene *Limnohyops priscus* shows no sinuses in a cross section of the parietal bone region (Osborn's fig. 254B). The legend is not clear as to the presence of pneumatization in this tapir-sized species, in which the top of the cranium is slightly concave, and a skull 375 mm. long; "In this primitive form the sagittal crest has not expanded into a flattened cranial vertex, and hence this region is without any *large* cavities" (italics mine).

II. Osborn had a 415 mm.-long skull of the Middle Eocene, broad-headed *Palaeosyops* sectioned — medially in the cranial region, and transversely in about the middle of its anteroposterior extent. The sections cannot be re-studied; they were made in the type of *P. leidyi* which is now an exhibition skeleton. In the cranium (Osborn's fig. 254 A1 = our fig. 12) the brain chamber occupies less than half the height. Thus the tabulae externa and interna are wide apart in the parietal and frontal bones. Osborn's legend to this figure notes "the cellular character of the expanded cranial vertex above the brain chamber". A large mass of bone lay above the brain. It was anteriorly, in its mid-height, invaded by a sinus which pneumatized about half of the dorso-ventral thickness of the frontal bone. Of course only the mid-plane configuration of this frontal sinus can be seen in the section. The sinus ended posteriorly over the anterior slope of the cerebral chamber. Two small bones are seen next to the skull roof, one below the other, about 32 and 36 mm., respectively, posterior to the transverse plane of the tip of the postorbital process; these are possibly fragments of an anterior sinus wall.

The transverse section through the right half of this skull (fig. 254 A2 = our fig. 13) was cut just behind the postorbital process and the last molar. The largest cavity in this section (not labelled) is the nasal tunnel. From its lateral wall thin plates variously extend into the lumen. These are remains of turbinates, and the small chamber which the dorsolateral ones enclose was presumably the cavity in the nasoturbinal. It is labelled "lateral ethmoid sinus" but obviously was nasal, not paranasal. Thick bone roofs the nasal chamber. It contains medially a small sinus (not labelled). This was probably the frontal sinus which the longitudinal section revealed in more posterior regions, narrowed and much flattened in the region of the cross section where it overlies the olfactory organ. Lateral to it a wider cavity is seen in the cross section, and this is labelled "frontal sinus".

Endocasts of this lateral postorbital sinus are present in *Palaeosyops robustus* AMNH nos. 1554 and 19234. The major piece of the latter specimen is an uncrushed cranium. This is about 220 mm. long, measured dorso-medially from the occiput to the irregular cross break which forms the anterior end of the fragment. The break is in the inter-orbital region. Along the break the whole interior of the skull is nasal chamber — that is, neither the dorsal nor the lateral sinuses extend so far forward. Backward from the break, for about 70 mm., the tabula externa ossis frontalis is lost in the lateral regions. This circumstance has revealed, to the right and left, beginning about 30 mm. behind the break, perfect endocasts of sinuses imbedded in thick diploë. Of course neither of the two endocasts is completely exposed; but their shapes suggest that very little is hidden under bone. Irregularly egg-shaped, the right and left sinuses are rather different in detail. Approximate breadth can be measured on the right sinus;

it is 20 mm., which was about one-seventh of the skull breadth in this region. This sinus is 41 mm. long. The left one extends farther forward, is 52 mm. long and up to 30. mm. high. The surface of the endocasts is quite smooth; these sinuses were not chambered. They had diverticula which were different in the right and left one, but each endocast has its most laterad projection near its anterior end. Comparison with other skulls (skulls whose lateral bones are preserved) shows that this anterior diverticulum projected into the proximal part of the postorbital process. The sinus did not reach forward into the roof of the orbit itself. Neither did it occupy the "strong median convexity near the fronto-parietal junction some distance behind the orbits" which Osborn mentions among the characters distinguishing *Palaeosyops* from *Limnohyops* (1929, p. 302). As seen in the uncrushed cranium here discussed, and likewise in Osborn's figures of *Palaeosyops* skulls and heads, the roof region he presumably was referring to is not an upward convexity; it is rather the rounded slope which connects the posterior, horizontal part of the skull roof with the lower, muzzle region containing the orbits. This is where, it seems, discrepancies occurred between the outer skull and the contained organ, so that pneumatic spaces developed. In contrast to the wide sinuses which large dogs have in the comparable region (see p. 440), those of the far larger *Palaeosyops* were restricted to the lateral margins of the skull. It is possible that this pair of small lateral sinuses near the anterior edges of the frontal bones was connected with the more median dorsal cranial sinus (fig. 12). However, both the specimens showing endocasts of the antero-lateral sinuses suggest that this cavity was a separate development. It is very similar to "Höhle 4^1" in Paulli's *Tapirus* (1900, p. 183, fig. 2) which, however, is one of four paired cavities pneumatizing a considerable portion of the frontal bone.

The other specimen exhibiting a sinus endocast is AMNH 1554, the skull whose dorsal aspect is shown in Osborn's fig. 285, and whose left fronto-nasal junction was sectioned (Osborn's pl. XVI, A1 and A2; our fig. 14). The right side of this skull contains a sinus endocast very similar to those described above. The tapering ends of the endocast suggest that sinus length was little more than the exposed 28 mm. Maximum breadth is 29 mm., which is about one-tenth the breadth of the flattened skull roof in which the cast is imbedded. In this crushed specimen the sinus lies in the region above M^3 and M^2 and partly over the orbit.

The only reference to *Palaeosyops* sinuses I could find in the text of Osborn's monograph is, indeed: "a prominent convexity above the orbits covering a large frontal sinus". This feature is no. 2 in the enumeration of the characteristics of the genus (p. 315). Characteristic no. 3 is: "rudimentary osseous horns which appear on the side of the face" — namely, as stated in an account of horn evolution in the titanotheres (p. 790), also "immediately above the orbits". Thus *Palaeosyops* is described as having had two swellings on each orbit roof, one pneumatized, the other not.

In order to save later students the trouble I had in finding either of these prominences (on *Palaeosyops* skulls, or the respective data in the labyrinthine monograph), I wish to state here that I found only one, a very slight, or no protuberance in the orbital region of the AMNH *Palaeosyops* skulls. The no. 2 feature of the list quoted above I have not found mentioned anywhere else in Osborn's text, nor is it pointed out in any of Osborn's figures. On the other hand, the horn rudiments of *Palaeosyops* play a large role in the monograph. Thus it is characteristic no. 2 which does not exist — or, rather, is identical with no. 3. This rudimentary horn, therefore, should be "covering a large frontal sinus". The sinus, we have seen, exists, although in a postorbital rather than supraorbital part of the frontal bone. As concerns the osseous convexity, it is apparent from Osborn's own descriptions that one can either not see it at all, or not see it as an incipient horn unless one's mind is preoccupied with the large horns developed by later titanotheres.

"Horns originate invariably above or slightly in front of the orbits, on the line of the nasofrontal suture" (p. 790; "at the junction of the frontals and parietals", p. 816, is a lapsus calami). However, in *P. robustus* AMNH 1554 most of the region marked "horn swelling" (fig. 285) is post-orbital; and the "horn swelling" of *P. robustus* AMNH 1580 is shown (fig. 286) on the medial half of the frontal bone — not above the orbit but above the nasal channel. The incipient horns further vary from "excessively rudimentary swellings which in their initial stages can hardly be detected" (p. 814) to the "distinctly rugose frontonasal horn swellings" listed as one of the characteristics of the species *P. robustus* (p. 331; also p. 790: "*Palaeosyops robustus* shows a rounded bony horn rudiment, which becomes quite conspicuous in aged individuals"). "Rudiments of horns are smooth and rounded" (p. 790) or, in "some very old males of *Palaeosyops* show . . . roughening of the outer tabula of the bone. (See Pl. XVI.)" (p. 266).

The figure Osborn is referring to is reproduced in our fig. 14. Even in that specimen roughening and protuberance can rather be felt than seen — but a description of what Osborn had in mind is found on p. 790 of this monograph: "bony exostoses or thickenings of the outer bony layer, with expansion of the cancelous tissue beneath". I can sinuses (and also paranasal sinuses with each other). The opening might be due to post-mortem disturbance; but the area as a whole appears undisturbed, as its general structure is the same in the right and left skull halves. Turbinals in the parietal bone region, and lateral instead of median to sinuses, would be a very unusual condition. Backward extension of the nasal cavity can shift a large number of not find the tabula externa thickening, and wide expanses of cancellous bone are not restricted to this particular region of the *Palaeosyops* skull. On the other hand, it is this region — the region at the post-orbital process — in which the diploic area is interrupted by the imbedded sinus. The smooth surface, which Osborn's figure shows on the lower side of the frontal bone section (our fig. 14, arrows) roofed the anterior region of the sinus; the sinus endocast is still present on the sectioned and figured left side of this skull (but not as well preserved as that on the right side). Thus there was a topographical relation between the supposed horn rudiment and the dorso-lateral sinus of *Palaeosyops*. The relation was, however, of course not functional. The only specimen whose sinus was figured in the monograph (fig. 254 A 2 — our fig. 13) is the type of *P. leidyi* of which Osborn particularly notes "the absence of any horn rudiments" (p. 328).

To summarize: Pneumatic spaces in the voluminous roof of *Palaeosyops* skulls have been found up to now 1.) dorsally in the region of the anterior brain chamber and posterior nasal cavity, 2.) dorso-laterally at the transition from cranium to muzzle, immediately behind and possibly also over the orbits.

III. *Dolichorhinus* of the Upper Eocene had a long, slender skull. Extensive pneumatization was developed despite the fact that, excepting greater skull lengths, none of the features commonly regarded as inducing pneumatization is added in this phylum, compared with the Palaeosyopinae from whose base it developed. There is, in fact, a loss of one such feature, viz., robustness of the skull — for example, breadth across the zygomatic arches is in *Dolichorhinus* absolutely less than in *Palaeosyops*. The "relatively prominent supraorbital horn swellings on nasals" (Osborn 1929, p. 396) are almost invisible. The brain is in the longer head even more (as has been written of titanothere brains) "hidden away". The brain capsule occupies only one-seventh of the skull length, and at the highest vault of the cerebrum the heights of skull base, brain capsule and skull roof compare as 1 : 3 : 4. Such a negligible quantity as the *Dolichorhinus* brain cannot have actively contributed to sinus formation; but the incongruity between small brain capsule and large cranium is spectacular. The *D. hyognathus* skull which Osborn's fig. 254 shows sectioned paramedially is very much like an *Equus caballus* skull in outlines and in length (550 mm.). However, its frontal sinus extends much farther back than that of horses. Pneumatization in *Dolichorhinus* was, further, much more extensive than it had been in *Palaeosyops*.

Osborn's interpretation of the large sinuses he discovered is seen in the lettering of his figure, which is reproduced in our fig. 15. His only comments were 1.) in the figure legend (p. 299), "showing . . . the elongate fronto-occipital sinus" and 2.) in the account of *Dolichorhinus* generic characters (p. 396), "space above brain chamber filled with large air sinuses". Osborn's figure of the left side portion of the sagittally sectioned skull does not show a "median section slightly to the right of the median plane". The section surfaces of both "halves" are to the left of the midsagittal plane. At the anterior end of the brain chamber, the cranium is about 40 mm. broad in the left and about 50 mm. in the right half. In the latter (our fig. 16), the section surface is not altogether plane but some matrix has come off, revealing in situ fragments of the septum sinuum frontalium. In these median and paramedian planes of the *Dolichorhinus* skull, bone of considerable thickness is seen only in very restricted areas. The floor and back wall of the brain chamber, and its roof only as far forward as the cerebellar chamber, consist of thick bone with spongy interior structure. The skull roof proper is relatively thin in this posterior region. It thickens slightly anterad. The nasal bones have the greatest dorso-ventral diameter among the portions of the outer skull roof; they contain some diploë, but no sinus (the line which in fig. 15 runs obliquely downward from the tip of the nasal bone represents the border of the matrix left within the skull). The matrix which has replaced the olfactory organ takes up by far the largest part of the section surfaces. It encloses scattered remains of the turbinate bones, particularly along the floor in front of the choanae. Remains of the most proximal turbinates, the delicate ethmoturbinates, are preserved in situ; they radiate forward and upward from the roof of the chamber which contained the olfactory bulbs (fig. 16, E — as in *Canis!*).

Immediately posterior to these ethmoturbinates there rises from the roof of the cerebral chamber a median and perpendicular plate: a fragment of a septum (fig. 16, se.) medially dividing a pneumatized region which, 70 mm. high, extends through the whole upper half of the cranium. This fragment is broadly anchored on the brain capsule; its lowest region is about 3 mm. thick, its maximum height and maximum length are 20 mm. Its anterior border appears to be the natural that the septum sinuum frontalium was posteriorly attached to the perpendicular portion of the occipital bone. There is in this specimen no indication that the median septum continued upward and attached to the roof portion; if it did not in the living animal, this was an extremely odd condition for the large dorsal sinus compartment (S. 1 — the "Fronto-occipital sinus (sagittal)" of Osborn's figure). Further compartments within the wide pneumatic area are indicated by sectioned bone plates seen in the matrix. One such plate goes forward, parallel to the skull roof, from the upper rim of the septum fragment and anteriorly joins a similar, lower plate. The two enclose a much subdivided sinus region which tapers anteriorly and is about 180 mm. long (S. 2 — the compartment whose posterior division Osborn labelled "Ethmoidal sinus (lateral)"). The present specimen does not disclose how far the giant occipito-parieto-frontal sinuses extended forward over the nasal cavity. Another specimen, the *Dolichorhinus* muzzle fragment AMNH 1843, contains a cross break at the front end of the orbits. This plane was not reached by the sinuses: there is no other cavity than the nasal chamber. The two surfaces of the longitudinal section of the *D. hyognathus* skull show a definite border between nasal and paranasal cavities only in one small area — viz., where ethmoturbinates and basis of median sinus septum, attached to the roof of the brain chamber, are preserved in situ.

Many questions arise during the study of this parmedian section of a skull whose interior structures are so largely destroyed. They are mostly answered, as far as they concern the brain region of the cranium, by a transverse section Osborn had made of a smaller specimen, a *Dolichorhinus* skull about 445 mm. long. The anterior portion of the cross-sectioned skull is shown in posterior view in Osborn's fig. 254 D, with the note that the cut was made "near line A-A" of the figure we have reproduced in our fig. 15.

The posterior surface of the transverse section (our fig. 17) shows the same structures as the anterior surface. It is approximately parallel to and 70 mm. in front of the occipital planum nuchale. In the brain chamber some of the matrix is removed on the left side, and the osseous tentorium cerebelli is revealed (t.) Its upper rim is 12 mm. posterior to the section plane. The section, consequently, crosses a posterior region of the cerebral chamber. The cranial bones are very thick around the chamber, particularly above it. Three paired areas containing matrix interrupt the cancellate structure. These are:

1. The paramedian pair of fronto-occipital sinuses whose dorsal part was seen in the longitudinally sectioned specimen. These cavities (S. 1) are extremely high; they reach from the tabula externa down into the groove between the cerebral chambers. As in the longitudinal sec-

tion, they appear to be paired only in the lower part. Here, there is a median septum consisting of right and left plates with some cancellate bone between them. Its ostensible upper end, however, is splintered; further, in the longitudinally sectioned skull, fragments of the median septum are preserved at levels above that where the present septum breaks off; lastly, the roof of the sinus contains a median groove, 1 mm. broad, from whose right side there points down toward the septum a tiny fragment of a perpendicular plate. This appears to have been the upper end of the left plate of the septum. Considering this evidence in the light of the completeness of median septa in other mammals, one is inclined to assume that also in *Dolichorhinus* inner and outer plates of the parietal were medially connected, forming a very high and delicate median septum ("mesethmoid septum" of Osborn's figure) which was broken by the intruding matrix in both the sectioned specimens.

2. A lateral pair of cavities in mid-height of the cranial roof (fig. 17, S2). Osborn labelled these "lateral ethmoid sinus". In Osborn's cross section of the *Palaeosyops* skull, which is in a plane much farther forward, this name was given to the nasoturbinate cavity. The space so labelled by Osborn in the longitudinally sectioned *Dolichorhinus* skull (fig. 15), however, is certainly a sinus compartment, and presumably it does correspond to the left one in the present specimen. There is no reason to call this sinus "lateral"; in the longitudinal section it is seen next to the plane of the median septum (fig. 16, S2). On the assumption that the sinuses were similar in the two sectioned *Dolichorhinus* heads one can infer from the transverse section that the compartments in question diverged posteriorly. They are seen as posteriorly directed pockets in the transversely sectioned skull. Also, one cannot see why these long chambers should be labelled "ethmoidal"; in the transverse section they are pockets, in the parietal bone, of the very large frontal sinus.

3. The mid-height region of the cranium has a peculiar structure. The section reveals here (fig. 17, X) large lateral areas which are neither filled with the coarse matrix found in the brain chamber which they overlie, nor are they filled with fine matrix as exclusively as the pneumatic areas above and median to them. From the latter they further differ in that they are not encased in small-celled bone but extend laterad to the external plate of compact bone. Within these areas, Osborn notes "the remains of the ethmoturbinal scrolls". There are indeed here, scattered through the matrix, bone particles of various shapes, and one or the other does remind one of delicate turbinate lamellae. Further, the area in question is in open connection with the paramedian sinus — as nasal cavities are with paranasal

rim of the septum, but the posterior and upper borders are splintered. Presumably this plate was originally continuous with the similar, somewhat smaller plate lying 7 mm. above it (fig. 16, se.) The latter plate is clearly seen to have continued farther back before the skull was sectioned; it is posteriorly adjoined by an area of matrix bearing the imprint of perpendicular bone (fig. 16, se). This impression shows turbinates under the cerebral chamber (*Elephas, Glyptodon*), and a small-scale process of this kind occurs above the ethmoidal chamber in Carnivora; but a similar process involving such large supra-cerebral spaces does not seem to have been observed in any mammal. *Dolichorhinus* certainly was peculiar also in having upward-radiating turbinals, and a supra-cerebral sinus far larger than the brain cavity. Possibly a study by the serial section method will show that in *Dolichorhinus* the olfactory organ did extend posterad over the braincase to this extreme degree. However, the evidence at hand is not convincing. Besides cut laminae of bone, the section contains bony circles, ovals, and multangulars with indented sides: bone capsules enclosing matrix. There is a gradual increase of bone and decrease of matrix in dorsoventral direction; at the base of the area in question, its structure is the same as that of the ventrally adjoining bone, and I believe that the area was one of loose-meshed diploë.

The two skull sections we have discussed can not reveal the anterior extent of the fronto-parieto-occipital sinus of *Dolichorhinus*. Nothing is known as yet about the interior structure of the orbit region. Horns were not developed. Osborn listed "relatively prominent supraorbital horn swellings on nasals" among the generic characters (p. 396), and "horn cores very prominent" as a specific character of *D. hyognathus* (p. 409). However, the type of this species is a lower jaw, and the only skull Osborn figures is the sectioned specimen AMNH 1851. On this I could not detect horn cores; nor did Osborn have them indicated in the dorsal views of the specimen fig. 346 B and pl. LIII, fig. C — the side views fig. 349 and pl. LII, fig. A — the front view fig. 348A — or the "cross section" (outline) of the anterior orbital region fig. 255, E1.

In another Upper Eocene titanothere, *Diplacodon progressum*, Mr. Bryan Patterson has recently discovered a pair of anteriorly situated lateral sinuses. These are particularly interesting in the present context as they are, it seems, the anterior sinuses described above in *Palaeosyops*, greatly enlarged — in connection with horn formation. According to the sketches Mr. Patterson sent me, this *Diplacodon* sinus extends between nasal chamber and lateral skull wall. It begins at about the middle of the temporal fossa and extends forward beyond the orbit, at least dorsally. It is widest at the postorbital process (as in *Palaeosyops*). Backward from there, it consists in a slender and tapering diverticle. Over the orbit it is broad. Anteriorly, it tapers at the infraorbital foramen, beyond which reaches a short tapering diverticle. This is (writes Mr. Patterson) "A large, thin-walled, chambered sinus extending beneath and in front of the horn". For, in contrast to *Dolichorhinus, Diplacodon* belongs to the family which, "including upper Eocene forerunners of the Oligocene genera *Menodus, Brontotherium*", is characterized by "precocious development of horns" (Osborn 1929, p. 434).

To summarize: In the late Eocene, *Dolichorhinus*, with skulls externally similar to *Equus* skulls, had the upper half of the cranium pneumatized, at least medially, back to the occipital bone. By far the largest area of the skull's interior is taken up by the olfactory organ. In *Diplacodon* the antero-lateral sinus, which was small in the Middle Eocene form studied, was greatly expanded in correlation with the development of horns.

The type of cranial pneumatization developed in *Dolichorhinus*, viz., frontal sinuses extending to the occiput, is an exceptional occurrence. Where such high and pneumatic spaces above the brain chamber exist in Recent mammals, they appeared to be an advantageous development in connection with frontal bone horns (ox, giraffe), with a proboscis (elephant, pig), or the giant size of a horn-bearing head (rhinoceros) — that is, the phenomenon was explained by features none of which were present in *Dolichorhinus*. In this ancient titanothere, the discrepancy between skull roof and brain chamber must be due to the fact that, in the Eocene even less than in later times, brain expansion did not keep in step with the development of large skulls. At first thought one has a ready explanation of the extreme pneumatization in *Dolichorhinus*; wide spaces in the large cranium had no function and were therefore invaded by air sinuses. However, similar conditions had not had the same effect in the Middle Eocene titanothere described above, and the enormous crania of Oligocene titanotheres, too, were far less pneumatized than those of *Dolichorhinus*.

IV. The early Oligocene American end-branch of the titanotheres is represented by forms much larger than existed in the Eocene. Height to top of scapula was 1010 mm. in a *Palaeosyops leidyi* and 1030 mm. in a *Dolichorhinus hyognathus*; this height is 1900 in one, 2502 mm. in another mounted skeleton of the Oligocene *Brontops robustus* (Osborn 1929, p. 585) whose skull lengths range from 743 to 843 mm. (ibid., p. 480). In the Oligocene titanotheres a pair of nasal horns projected upward and laterad and/or forward from the skull. These horns vary from low bosses or short cones to structures of fantastic size and shape. Their cross sections are flat or wide ovals, triangles, circles. They stood over the eyes, on the front tip of the skull, or in an intermediate position. As the other characters on which the genera and the species were based have also been found to be so variable, Scott advised uniting in a single genus all the White River titanotheres (with one exception; 1941, p. 907). They are not descended from the Upper Eocene genus *Dolichorhinus* whose cranial pneumatization we have discussed, nor is *Palaeosyops* regarded as an ancestor of the Oligocene forms. However, they have evolved from early Middle Eocene members of the subfamily Palaeosyopinae (Simpson 1945, p. 255). We can, therefore, take the liberty of regarding as broadly ancestral the conditions found in *Palaeosyops*, viz., paramedian sinuses across anterior cerebral and posterior nasal regions plus small dorsolateral sinuses at the posterior end of the orbit. The latter sinuses we know to have enlarged in the horned Upper Eocene *Diplacodon*, a form in or very near the ancestral line of the Oligocene titanotheres.

I studied horns in the AMNH, YPM and MCZ, and the skull proper mainly in two specimens of the MCZ collection of titanotheres from the Lower Oligocene White River beds of the Dakota-Nebraska-Wyoming region. Both are flat-topped skulls. (Many individuals had the occiput curiously drawn upward; the interior build of that superstructure remains among the several items still not studied.) MCZ 6729, labelled *Menodus proutii*, consists of numerous fragments among which are cranium (brittle), coalesced nasals, and one horn. MCZ 6226, labelled Titanotherium (a name now invalid), consists of large chunks making up most of a very large skull. The middle part is missing, also much of the nasals so that the relative position of the horn — the voluminous base of the left one is in situ — is obscure; an attempt to find a genus name seemed futile. This skull suffered distortion whose result is interesting in the present context. Skull roof and skull base have not been very much put out of shape. It was in the less solid mid-height region of the skull where diagenetic pressure took effect. The ventral regions are now considerably to the right of the formerly corresponding dorsal regions. The cross sections Mr. Stanley J. Olsen made of this distorted skull, therefore, do not represent exactly transverse planes.

Fig. 18 shows the structure of the occipital region. The section plane contains ventrally the anterior end of the left condyle, and dorsally it is 70 mm. anterior to the upper rim of the planum nuchale. This distance happens to be the same as that of the *Dolichorhinus* cross section but in the larger skull the plane is, of course, one relatively farther back. In the figured, posterior surface of the cut the brain chamber contained the medulla oblongata plus the lower posterior end of the cerebellum. Here, a brain region about 60 mm. high was encapsuled in a cranium about 210 mm. high. The thickness of the roof is medially as much as 105 mm. In the anterior surface of this cut — that is, in a plane 3–4 mm. in front of the figured one — the cranial roof is 90 mm. thick medially, laterally much less. Here is sectioned the wider chamber of the cerebellum, whose configuration explains the puzzling left dorsad and laterad evaginations of the brain chamber, and a separate patch of matrix, in the figured surface. They correspond to posterior lobulations of the left cerebellar hemisphere. The matrix-filled pocket seen descending from the left lower side of the oblongata cast continues in the anterior surface of the cut as a downward canal; it is the hypoglossal "foramen": a canal of considerable length in this bulky skull. In neither posterior nor anterior surface is there a trace of pneumatization of the vast expanse of bone surrounding the brain chamber. The area which in the photo shows darker than the external compacta is penetrated by matrix; it consists of tiny-celled diploë.

Fig. 19, shows this cranium sectioned 130 mm. farther anteriorly. Outside the cranium, the section passes along the anterior edge of the transverse part of the zygomatic process of the temporal bone. Within the cranium, an anterior region of the cerebral chamber is sectioned; the basal groove lodged the olfactory tracts, known to be a particularly prominent feature on titanothere endocranial casts. In contrast to the brain region of the more posterior section, the cerebrum occupied the whole breadth of the cranium. This is also the case in the *Menodus* specimen, in this anterior region as well as farther back where the cerebrum is broader. On the other hand in *Brontotherium ingens* YPM 14169 the cerebral chamber has thick lateral walls in the anterior region disclosed by a transverse section about 28 mm. behind the olfactory bulbs (in the endocast of this cranium the cerebrum is 108 mm. long). In none of the three specimens does the cerebrum extend through the whole height of the cranium. In our section, the cerebral chamber has a roof as high again as the chamber itself. It is not from this bulky bone that there stem the bone fragments seen scattered all through the chamber; they are splinters of the thinner, crushed side walls. The roof is massive as far laterad as to a point beyond the maximum height of each hemisphere. The frontal sinus extended back to the plane of this section, but only dorso-laterally, above the lateral slopes of the cerebrum. Directly over the lateral margin of the cast of each cerebral hemisphere there is a small area within the roof (fig. 19, S?), conspicuous because symmetrical, in which the bone is splintered. The left one contains some matrix. These areas are possible ends of paired frontal sinus diverticles. The left lateral border of the cranium contains a matrix-filled posterad sinus pocket (S.). This pocket is present, in the same location, both in our *Menodus* specimen and the *Brontotherium* YPM 14169; it represents the most posterior region of the frontal sinus.

The irregular breaks in the *Menodus* cranium allow one to follow the sinus farther forward. The olfactory bulbs were in a rather low position. A transverse break crosses their chambers in about the middle of their lengths. (Remembering the supposed ethmoturbinal scrolls of *Dolichorhinus* in a plane far posterior to the present one, we must mention that turbinates were not found here but begin farther forward in *Menodus*.) Maximum height of the bulbus chambers is 20 mm., that of the massive bone below them, 25 mm. Their roof, however, whose height is 30 mm. +, is bony only medially for about 15 mm. of its breadth, and laterally the roof is massive only in its upper two-thirds. In its lower third lie, over the bulbi, a pair of sinuses. Their smooth posterior walls, with posterad grooves here and there, recede obliquely latero-posteriorly. These perpendicular walls apparently continued to end in the most posterior pocket, that which lies lateral to the latero-anterior slope of each cerebral hemisphere. The frontal sinuses also extended downward along the lateral surfaces of the bulbus chambers. While this is only suggested by the conditions in the *Menodus* specimen, *Brontotherium* YPM 14167 shows chambered sinuses to the right and left of the olfactory bulbs. Thus, while over the anterior slope of the cerebrum the sinus is only a dorso-lateral pouch, it is wider and higher in the bulbus region. The configuration is comparable to that seen, among the Equidae, in *Merychippus*. Once again one recalls the comparisons between extant mammals which seemed to warrant the conclusion that within each order the degree of pneumatization is correlated with body and skull size. However, the two extinct perissodactyl forms with, it seems, similar pneumatization, were very different in size. Shoulder height in *Merychippus* averaged one-half, skull length one-third of that of the American Oligocene titanotheres. Also comparable to the cranial frontal sinus of these titanotheres is that of a similar-sized, recent form from another order, *Hippopotamus*; in the hippo, however, the surrounding diploë is not a tiny-celled honeycomb but a very loose meshwork, and there is another, a large anterior sinus which up to now has not been found in the Oligocene titanotheres.

The region anteriorly adjoining the bulbus chambers is in the two MCZ specimens partly lost, partly in fragments. There seems to have been a solid roof over the nasal chamber, but laterally there were apparently longitudinal pneumatic spaces such as Cope saw in "Symborodon". *Brontotherium* YPM 14169 shows that cavity in a plane about 220 mm. from the planum occipitale, i.e., about 45 mm. anterior to the cribiform plate. In the lateral walls of the ethmoidal labyrinth there is a small tunnel dorsally and a larger one in midheight. These are presumably anterior continuations of the cranial sinus. There is no dorsal compartment such as Osborn figures in *Palaeosyops* between the lateral ones (our fig. 13).

Still farther forward, where the lateral sinuses were broadest in *Palaeosyops*, those of the MCZ titanotherium are, it seems, narrow canals — namely, at the junction of the long temporal fossa with the orbit; this is where a third section was made across our titanotherium specimen.

Fig. 20 shows the anterior surface of this section, viz., a plane crossing the palate 280 mm. posterior to the tip of the premaxillaries. The configuration is not easily understood. In part this is due to the distortion and consequent breakage inside the skull. Besides, however, a region is represented whose topography in the titanothere is not comparable to any one skull region of well-studied Recent ungulates such as the horse (whereas conditions in the tapir, not studied, presumably are comparable). The plane of our section is so far anteriorly that behind it were about two-thirds of the skull. Its unfamiliar appearance is connected with a trend in titanothere evolution just the opposite of one observed in the Equidae. The orbits of the early titanotheres were, like those of the early Equidae, in the middle of the anteroposterior extent of the skull, above the posterior molars. In the Equidae the evolutionary elongation of the muzzle has not involved the orbit; their eyes remained close to the braincase and lie today posterior to the tooth series. In the titanotheres, on the other hand, the orbit shifted anterad (Osborn 1929, fig. 740); in our sectioned specimen the eye lay over the first molar and partly over the second.

We have cut between anterior surface of the M^3 and posterior surface of the M^2 crowns. This plane is in *Equus* well anterior to the orbit, in the titanothere behind the orbit. Horse heads have been transversely sectioned in an ostensibly corresponding plane, passing between M^2 and M^3, by Baum (1894, fig. 5), and slightly farther anteriorly, across the posterior part of M^2, by Sisson (1940, fig. 455). Those sections cross, besides the nasal passages, the large maxillary sinus and its extension into the ventral turbinate, the frontal sinus extension into the dorsal turbinate, the naso-lacrimal and other canals — including the infraorbital which in the titanothere begins 120 mm. anterior to our section.

Our cut crosses the postorbital process near its posterior surface. In the titanothere this process is a hardly noticeable laterad stump next to the anterior end of the frontal bone, but in *Equus* it is a large structure bracing cranium and zygomatic arch. Baum's section near the posterior surface of the postorbital process in *Equus* (1894, fig. 7 — a plane far posterior to that of his fig. 5!) is partly reproduced in our fig. 3C. The horse skull here contains the wide frontal sinus of the anterior cranium, the olfactory bulbs, and the last turbinate scrolls above the pharynx. The titanothere section also crosses the junction of temporal fossa and orbit, but it is in the mouth region. The cavities within the skull must all have belonged to the nasal system. Our problem is to decide to what extent they were paranasal, that is, sinuses.

Incidentally we have to mention, as another example of the massiveness of late titanothere bones, that there is not a trace of a maxillary sinus here, in the plane where M^3 and M^2 adjoin. The large antero-lateral root of the enormous M^3 is implanted in massive bone — so deeply implanted that directly above it, where horses have the maxillary sinus, there is in the titanothere the temporal fossa. However, in a maxillary bone fragment which lay over the posterior parts of the M^3, there is medially some matrix. Thus there seems to have been a maxillary sinus in our specimen which ended posterior to the plane in which our section crosses the maxillary bone — viz., over the postero-medial root of the last molar. In any case, Mr. Patterson has discovered and will describe just such a sinus in another gigantic Lower Oligocene American titanothere, *Teleodus*.

The lower region of the sectioned fragment ends medially with the palate of the left side; but due to the distortion of the skull the section includes dorsally, above a vast matrix-filled cavity, not only the left nasal bone, but also part of the right one. Thus the midline of the coössified nasal bones can be identified, and it is seen that four pairs of grooves channel their lower surface. The ridges which separate these grooves all end ventrally with broken surfaces. Fragments of bone, narrow in the section, are scattered through the matrix — remnants of laminae which originally continued the ridges. This is particularly clear in the case of the largest of these fragments, whose broken upper end still lies close to the broken median ridge. It is the upper part of the septum nasi which, in life median and perpendicular, went down to the midline of the palate where it stood between the two ventral meati of the nasal channel. The floor of the left ventral meatus is preserved in the specimen, as it is the dorsal surface of the palate. Next to it lie three delicate fragments of the roof, remnants of the left ventral turbinate.

The ridges on the ventral side of the nasal bone are all triangular in section, with rounded sides. This is, I believe, significant — the characteristic attachment of turbinates in contrast to that of sinus septa. Practically all the plates I have seen projecting into sinuses do not have rounded but angular attachments to the main bone tabulae. Such angles are highly variable, whereas the ridges in question are regular. Further, the septa within a sinus pair are rarely, if ever, symmetrical. It follows that the large cavity seen in our section is nasal, at least as far as it was roofed by the three more medial pairs of the four symmetrical grooves. These three roofed nasal channels: next to the midline the dorsal meatus (fig. 20 : 1), lateral from this the cavity of the dorsal turbinate (2), and the third the cavity in the ventral turbinate — if conditions in the broad titanothere muzzle were indeed similar to those in the high muzzle of the horse. Horses have between dorsal and ventral turbinate a narrow middle nasal meatus; this may well have been wide in the titanothere.

Identification of the fourth groove must be left to the proposed study of a whole skull in serial sections. This lateral pocket (4) may represent another turbinate cavity but even so, if it was closed anteriorly, it may have been functionally a sinus as are the posterior part of the dorsal turbinate and the ventral part of the ventral turbinate in *Equus*. There may also have been here a genuine sinus compartment. Perhaps the quadrangular piece of bone, which now lies horizontally below the ridge limiting cavity 4, was originally connected with the ridge. However, this appears improbable because that fragment is far thicker than the ridge.

The fragment in question is a part of a weirdly branched and broken thick plate which crosses our section between nasal cavity and temporal fossa. Of course this plate must be, or include, the wall of the temporal fossa; but it was crushed down, and at least its lateral part appears to have been telescoped during the distortion of the skull. Its various processes cannot be identified on the evidence of this one section. They were not necessarily directed in life upward and downward as they are now oriented; for the "plate" may be twisted, or it may have been rotated as a whole at the break seen above the hollow labelled "6".

This hollow opens ventrally towards the temporal fossa; but any reader intrigued by the details of fig. 20, and disappointed with my diffidence in explaining every one of them, will please consider that cavity "6" in the section presumably represents a closed canal, and that such a canal might have contained any one or several of nerves II, III, IV, V^1, VI and/or blood vessels, or even the naso-lacrimal duct. In horses this duct leads anteriorly from the orbit into the nasal cavity, whereas our section is at the posterior end of the orbit; but the horses' tears are discharged behind the tooth battery, whereas our section is across the tooth region of the titanothere.

A lateral prong may have been the proximal wall of a cavity (5), and such a cavity would have been a postorbital sinus. One definitely pneumatic cavity is revealed in our section (fig. 20 : S.). Its lower wall is lost; a bone fragment lying nearby in the temporal fossa matrix, triangular but with one concave side, may have been part of the floor. This sinus is lateral, small, smooth-walled. It is separated from the large and complex cavity described above by a thick sheet of perpendicular bone. The sinus endocast consists of fine-grained stone and thus is strikingly different from the coarse matrix in both nasal cavity and temporal fossa. Thus our titanotherium had a small sinus at the postorbital process. Its latero-dorsal position and its shape are so much like those of the pneumatic canals observed more posteriorly that continuity is strongly suggested. In another skull, YPM 14168, a sinus is seen in the posterior part of the orbit roof, pointing backward towards the postorbital process.

From the specimens I have seen I had the impression that the long, narrow, latero-dorsal pneumatic space has its anterior end in the posterior orbit region — perhaps at the anterior end of the frontal bone. However, my impression is deduced from material which, it must be said again, could not furnish a complete picture of pneumatization in the Oligocene group of titanotheres. Further, variation was great. Sinus configuration must have been particularly variable in the skull region anterior to our third titanotherium-section. In those individuals which had supra-orbital horns, the horn sinus mentioned by Marsh must have been confluent with the sinus just described; thus, the entire orbit roof must have been pneumatic. But other individuals had the horns more anteriorly; in some, the horns were terminal in position, standing on the very tip of the nasal bones (fig. 25) so that the usual anterad nasal shelf (fig. 23) had disappeared. In no one of the specimens available to me for study are all three elements — orbit, nasal shelf and horn — present and broken appropriately for sinus study. The *Menodus* MCZ 6729 fragments include the nasal shelf and one horn; however, the two pieces do not fit together. Therefore the following description of nasals and horns treats separately what surely were two pockets of one sinus — two pockets which, it will be seen, were reduced to one when the nasal shelf was "swallowed" by the horns.

The nasal shelf is solid. Here was a balcony-like structure, a free projection in advance of the horns, overhanging the nasal orifice. It is comparable to that of the rhinoceros, but is broader and stouter. In lateral view, dorsal view (fig. 23) and cross section (fig. 24) it is practically square. The nasal shelf of the rhinoceros tapers to a pointed tip, and it is completely pneumatized — the larger "superstructure" of titanotheres consists of bone throughout, like the corresponding, but very slender structure of the horse. The state of nasal bone fragments in our collections graphically attests to this fact. The shelf broke off as a whole. Such fragments end posteriorly at or just behind the anterior limit of nasal bone pneumatization; their posterior surfaces reveal a more or less shallow anterad pocket in each nasal bone.

For example, the nasal shelf fragment of "Titanotherium" AMNH 32510 ends posteriorly in an irregular transverse break whose maximum distance from the anterior tips of the nasal bones is 160 mm. In this plane much of each nasal is pneumatized. In the cross break, each nasal contains a roundish sinus which is separated from its opposite by an hourglass-shaped column of bone. This, the median "septum", is narrowed in mid-height to only 11 mm. About 50 mm. farther anteriorly in this specimen the sinuses end. Between the end pockets there is bone with a minimum width of 36 mm. In that transverse plane, total breadth of the shelf is 145 mm. At the anterior margin this thick, solid, 110 mm.-long plate has hardly narrowed; it is 125 mm. broad.

The nasal shelf fragment of *Menodus proutii* MCZ 6729 clearly shows that it was just this squarish projection of the nasals which was solid, and that the sinus end pockets lie where the nasal bones broaden to carry the horns. This fragment is 110 mm. long. Back from the rounded tips, these coalesced nasal bones have parallel lateral borders for about 75 mm. of their length and are 130 mm. broad. Behind this shelf portion the borders diverge (towards the anterior margin of the horns), and the fragment is 170 mm. broad at its posterior end (fig. 24). A broad median region of the fused nasals consists of bone. To its right and left are shallow pneumatic pockets which continued latero-posteriorly beyond the borders of the fragment. These pockets were the anterior ends of a sinus pair whose posterior end we do not know. It is possible that there was only one pair of latero-dorsal cavities, continuous from the anterior cranial region to the front of the muzzle. More probably, there was here a separate paranasal development as peculiar to the titanotheres as are their horns.

The transverse plane in which the solid part of the nasal bones ends posteriorly is that where the horn region begins. As said above, I have not actually seen the sinus in the body of the nasal in connection with that in the hornbase. However, the horn of *Menodus* MCZ 6729, broken from the nasals just described, is pocketed all across its base. There is no indication of even a partial septum setting off this distal pocket from the proximal one. The hornbase sinus appears to have been an upward-laterad outpocketing of the sinus in the adjoining region of the skull proper, i.e. that in the horizontal part of the nasal bone. The pocket in the horn, while wide, is usually shallow. The present *Menodus* horn, for example, is of the bulbous kind, but its sinus did not reach up to the level where it increases in circumference; of its 225 mm. length, only 40 mm. is pneumatized. Naturally, there was great variability. In our sectioned horn specimen (fig. 21), whose base may not be completely preserved, one-fourth of the length is pneumatized.

It follows that the heaviness of titanothere horns is only to some extent due to the fact that we handle them in a fossilized state. They must also have been extremely heavy when carried on the living heads. Like the nasal shelves, these horns were largely solid. The horn MCZ 11698, which we have sectioned (fig. 21), is of the sub-conical, round-based type which rose behind a nasal shelf. It is filled with small-celled spongiosa. The streaks of dense bone seen in the section must have been either columns or walls of compacta within the diploïc mass. Smooth compacta walls off the basal sinus—evenly vaulted in this specimen; in other horns such sinus pockets are partly subdivided by one or more irregular, low ridges (fig. 22).

It is odd that practically no notice has been taken of these hornbase sinuses, for they are quite conspicuous features in the majority of isolated horn specimens. In the collections I have visited are some titanothere horns broken by chance at various levels; naturally, this mass of cancellate bone with its thin coat of compacta is as likely to break at one level as at another. However, most horns are broken from the skulls in a manner obviously correlated with their particular kind of pneumatization. In significant contrast to the condition in which paleontologists find the horns of broken cavicornian skulls, a titanothere horn specimen is usually a horn from tip to base — the whole horn, and nothing but the horn. It is usually broken from the remainder of the nasal bone in the only plane in which it consists of relatively thin bone, namely, where its sinus is widest: at the junction of horn and skull proper. The sinus is a conspicuous feature in such fragments because its wall is the only finished area of the whole surface. Further, while in relation to the horn the basal pocket is small, like everything in those giants it is absolutely large. At the proximal end of the *Menodus* horn MCZ 6729, the maximum diameters of the horn base sinus are 140 and 75 mm. Only at their roots were the horns really hollow. Regardless of the horn's form, the sinus rapidly tapers distally in the majority of cases.

As said above, it was Marsh who discovered these hornbase sinuses, and he called them "large" (1876 b, p. 335). Indeed Marsh's YPM collection contains three horns in which the sinus reaches unusually far up. While two of them represent extreme variation towards large size of the horn sinus in adults, the extent of the sinus in the third specimen is possibly related to young age of the individual. One horn of YPM 14170 is broken lengthwise, revealing the endocast of a sinus rising through the proximal half. Another large horn, YPM 14171, with a 100 mm.-diameter at the base, is preserved as an 85 mm.-high stump; at the level of the break this horn contains a central cavity 42 mm. wide (strangely, not seeming to be connected with that in the hornbase). YPM 14168 is a small skull in fragments. The more complete one of its conical horns is only 120 mm. long; through half its length goes a wide, partially subdivided sinus pocket. This young horn is an interesting illustration of differences between horns developed in the early Oligocene and the cavicornian horns of later times. In the ontogeny of Cavicornia the sinus expands at a greater rate than the horn core grows, so that older horns are more hollow than young ones. One is not judging from only the one young titanothere horn when one believes that in that group there was very little sinus expansion while the horn was built up to enormous size; this is also clear from the condition of the adult horns. We have quoted above (p. 454) Andrews' description of *Arsinoitherium* horns; it suggests that in these horns, too — but on a smaller scale than in the present case — the solid bone portion increased during ontogeny instead of becoming thinner as it does, at least relatively, in Cavicornia.

Following Osborn's reasonable assumption that the titanotheres with terminal horns have evolved from forms with lateral horns, we find reduction of pneumatization also in phyletic evolution.

Brontotherium platyceras (fig. 25) was the largest among the American Oligocene forms (a skull is 880 mm. long). It "represents the climax of the evolution of the long-horned titanotheres" (Osborn 1929, p. 579). Its nasal bone sinus, however, is not larger than in the forms from which it has developed. Naturally, the nasal sinus of *B. platyceras* extends farther forward to reach the anteriorly placed horn-bases; but it has lost the pockets which in the forms described above pneumatize the hornbases.

B. platyceras MCZ 9160 consists of the horns and the horizontal plate of the nasals, which is preserved in a (maximum, median) length of 190 mm. The irregular transverse break at the back end of this specimen slopes antero-ventrally. In this section are seen a pair of sinuses. They are wider than in the more posterior plane shown in fig. 20, but even so they do not make the nasal bones hollow as is the case in rhinos; they lie to the right and left of the choana roof. On the level of the greatest width of these sinuses, the coalesced nasal bones are 180 mm. broad, the left sinus 32 mm., the right one 39 mm. Both are oval in the oblique section which the break has produced. A line continuing the axis of each horn downward through the skull roof would be the long axis of the sinus oval. But there was no outpocketing towards the horns of these dorso-lateral longitudinal pneumatic channels — neither in this transverse plane where the horns had stood in ancestral species, nor farther anteriorly where rise the gigantic horns of this form. In the *Brontotherium platyceras* nasals we find not two pairs of tabula interna vaults but only one pair — the anterad pockets in the center of the body of each nasal bone (fig. 22). This has "swallowed" the horn-base sinus. In this species, "The connecting crest between the horns has grown to such a height and the horns to such a breadth that in front view the head terminates in a great vertical plate 6.75 inches deep and more than 18 inches broad at its widest part" (169 mm. and 450 mm., respectively; Obsorn 1929, p. 579). It is not possible to draw, across this plate, lines exactly separating the horns from the connecting crest (which consists of the anterior ends of nasal bones not projecting in advance of the horns). However, it is clearly seen that the pneumatic pockets are in the middle part of the crest-horns-complex. Characteristically, the right and left pockets are quite different. A ridge divides the left one into two pockets, one of which has two narrow anterad diverticles; the end-pocket of the right sinus is one smooth anterad vault next to the anterior end of the nasal bone. The horns of *B. platyceras* arc, consequently, solid throughout.

The *Brontotherium* fragment whose posterior surface is here described and figured (fig. 22) is the type of *Menodus platyceras* Scott & Osborn 1887. With the original description (p. 160–163) this specimen, MCZ 11214, is figured (fig. 4) in anterior and in lateral views, with an outline (called "section") of a horn in dorsal view. Osborn's monograph (1929) repeatedly refers to this specimen. The original description ("Scott and Osborn write") is quoted p. 221–222 with fig. 178. The diagrammatic "section at base of horn" is seen in figs. 375G, 399, 458 and 481A, and the latter figure also contains the outline of a horn in medial view. The general description of the species, now called *Brontotherium platyceras*, mentions "the type horns in the Harvard museum" p. 579. Their estimated external length is given as **400** *mm.* on p. 553. Since Osborn described (p. 221) as the inner contour of the horns the posterior one, "Outside length of horns, **315** *mm.*," (p. 222) should be the anterior length and thus identical with "Length of horns measured from tips to median fronto-nasal suture, **250** *mm.*" (p. 161 in the 1887 paper, from which the 1929 passage purports to be quoted). The opportunity is taken here to point out that in the type specimen 315 is the correct measurement and that, further, it is length of horn plus one-half "crest".

Looking back over this first and very incomplete survey of pneumatization in titanotheres, one can venture the following tentative outline of origin and evolution of frontal sinuses in this diversified group. The titanotheres evolved from the same perissodactyl root as the Equidae with, consequently, un-pneumatized skulls. The earliest genus of whose pneumatization we know is the Middle Eocene *Palae-*

osyops. This form was already large-skulled and still small-brained, as were the later titanotheres. Two paired sinuses were found in the frontal bone. One lies across and in front of the anterior slope of the cerebrum, the other over and behind the posterior end of the orbit. In the phylum which did not develop super-structures on the skull, excessive pneumatization hollowed the upper half of the cranium in the Upper Eocene *Dolichorhinus.* In the phylum which developed giant animals with gigantic horns, the greater part of the vast cranial roof was massive in the Lower Oligocene end-forms. The frontal sinus had its main area, as in *Equus,* around the olfactory bulb chambers. Tapering pockets, smaller than the supra-cerebral sinus of *Palaeosyops,* extended back to the latero-anterior slope of the cerebral chamber. Anteriorly, the sinus narrows to a dorsal channel inside the lateral margin of the frontal bone. It either ended in the posterior part of the orbital region or was continuous with a similar sinus in the nasal bone. In forms with lateral horns, the nasal bone sinus evaginated into the horns; but it failed to pneumatize either the horns or the large nasal bone shelf in front of the horns. In forms with terminal horns, the lateral evaginations have disappeared.

On pl. IX we show the dorsal aspect of an entire *Brontotherium platyceras* skull, the anterior end above, alongside one of *Bos taurus* in opposite orientation. There is a striking similarity of outlines. The brontothere horns enlarge the anterior end of the head much as the ox horns enlarge the posterior end. The solidity of the Oligocene horns graphically illustrates the weakness of overall theories based on so small an assemblage of mammals as are the Recent genera. Anatomists studying Recent mammals are under the impression that air sinuses actively develop whenever a heavy skull, wherever a superstructure needs to be lightened. Should not horns on the very tip of the roof of the necessarily hollow nasal chamber have more need of being pneumatized than horns broadly anchored on the most voluminous region of the skull? Would it not have been "easier" for pneumatization to extend into horns situated in the immediate proximity to the channel through the head which supplies the air for all pneumatization than in the case of horns which stand on the far-away occiput? Actually, it is the latter which are hollow, not the nasal horns of the Oligocene titanotheres.

As long as we know no more about the sinuses of titanotheres than the data assembled in this chapter, two lines of speculation are open regarding the solidity of the Oligocene titanothere skulls.

In the evolutionary history of other mammal groups we have seen that skull pneumatization is a progressive feature. The titanotheres, however, were a group in which, "Although the later members were spectacular animals, the amount of fundamental progress, variety and important novelty . . . was slight" (Simpson 1945, p. 255). With regard to frontal sinuses, the Dolichorhininae did achieve important novelty, but in the brontothere line not even the development of giant size increased the degree of pneumatization.

On the other hand, it appears that the cranial frontal sinus was relatively larger in a Middle Eocene ancestor than in the Lower Oligocene forms, and the sinus under the horn seems to have been more extensive in an Upper Eocene ancestor. The Oligocene condition thus may have to be regarded as secondary—as a result of the trend towards solidity of the entire skeleton in the phylogeny of the titanotheres.

I have not found any specific data on the inner structure of the post-cranial bones in the pre-Oligocene forms, but we know that in the Lower Eocene only were the titanotheres as light-limbed as the Equidae. Already in the Middle Eocene "these animals were heavier bodied and slower moving of limb than the modern tapirs" (Osborn 1929, p. 608). In the Oligocene, the post-cranial bones were solid. According to Scott (1941, p. 874 — on characters of the Oligocene forms), "the skeleton underwent an adjustment to the mechanical needs of supporting great weight, the long bones loosing the marrow-cavities, which became more or less filled with cancellous bone." However, that trend does not appear so advantageous when now we realize that it was not restricted to the long bones. In the skull, the trend towards solidity apparently reversed the tendency observed in the majority of mammalian phyla, viz., expansion of pneumatization during size increase. Except in the nasal area which carried the horns, the gigantic Lower Oligocene skulls were less pneumatized than smaller skulls from the Middle and Upper Eocene.

The fact that a comparable trend towards massiveness is observed in two water-adapted groups is another difficulty in the interpretation as an adaptive feature in titanotheres. Granger and Gregory speak of "the pachyostosis of the horns" of certain late titanotheres (1943, p. 367). But it is the pachyostosis (so called after the disease which in human bones obliterates the marrow cavities) of Mesosauria and Sirenia which has fascinated the paleo-endocrinologists, headed by Nopcsa. Pachyostosis seemed, in evolution, "to begin always in a certain stage of adaptation to aquatic life, and it disappears later on" (Nopcsa 1923, p. 116). In the phylogeny of the Sirenia pachyostosis has continued to increase, but this is easily explained by the iodine in the algae the seacows feed on . . . (ibid., p. 117). Nopcsa and some of those who discussed his ideas at the 1922 meeting of the Paläontologische Gesellschaft (Paläont. Zeitschr. 1923, vol. 5, p. 258–265) found that practically every evolutionary development of phenomena which in man result from diseases benefits the animals concerned. Unfortunately, titanotheres were not included in that discussion.

Rhinocerotidae. The largest of living perissodactyls are comparable to the late titanotheres insofar as they are giants and carry one or two horns on the nasals. Their skulls, however, are extensively pneumatized. The frontal sinus of the two-horned *Ceratotherium* (Paulli 1900, figs. 4–5 and pl. VIII) pneumatizes the whole skull roof, from the tip of the nasals to the back of the occiput. According to Weinert (1925, p. 266), this is the condition in all extant rhinos.

In the case of the Rhinocerotidae fossil evidence shows even more distinctly than the case of the titanotheres that, contrary to current opinion, the development of horns was not decisive in the development of pneumatization. The huge paranasal sinuses antedated the origin of the horn-bearing osseous protuberance. The influence of the horn on the sinus was limited to the immediate proximity of the horn. The extinct genera follow each other in time, but they are not ancestral to each other or to *Ceratotherium.*

As in the Equidae, frontal sinuses were late to develop. *Hyrachyus princeps* of the late Middle Eocene is the largest species of that genus, a complete skull being 346 mm. long (Wood 1934, p. 281). *Hyrachyus* cf. *princeps* YPM 12529 is a cranial roof which ends anteriorly in breaks of various directions above the ethmoidal chamber; a right side break reveals, further, the interior structure of the frontal bone roof of the anterior cerebral region. The whole space between tabula externa and interna, 20 mm. high at the ethmoidal windows, is filled with spongy bone. "In the ancient Rhinoceroses of America there is no diploë; the osseous cranial wall is solid in the Oligocene Aceratheres and even in the Upper Miocene *A. fossiger*" (Osborn 1898, p. 119). Of another hornless predecessor of the living rhinos, the Mio-Pliocene *Chilotherium* (skull lengths 490–541 mm.), there exists a natural endocast of a whole Upper Miocene skull (Edinger 1937). Here the frontal sinuses are very extensive, similar to those of the Pleistocene and Recent rhinos. As in these forms with steeply rising parietals and a very high occiput, parietal and occipital bones were pneumatized in *Chilotherium,* whose skull roof was almost flat. The nasal bones, however, were horse-like in the hornless Mio-Pliocene form. Thus it seems that in rhinoceroses the nasal bones became pneumatized only when their outer plates bulged upward to provide the horn base. Brandt (1849) has given a striking figure (pl. XVIII) of pneumatization in the Pleistocene *Coelodonta antiquitatis,* and a graphic description (p. 283–284); "the air cells are so large and numerous that almost all the bones of the skull are, by their cellular cavities, connected with the nasal cavity". The nasal is not mentioned among the pneumatic bones which Brandt lists by name, and it is not sectioned in his figured specimen; but he mentions (p. 268, 283) large air cells in the posterior and basal parts of the bone distinctive of the species, the ossification of the nasal septum under the horn.

Even from the scant material described in the literature it is clear that the various branches of the rhinocerotoid evolutionary "bush" acquired pneumatization at different times. Different reasons can perhaps be found. The "Upper Miocene *A. fossiger*" Osborn refers to in the statement quoted above is *Teleoceras,* Upper Miocene or Lower Pliocene in age; but it does not seem to have developed the braincase pneumatization which was found so extensive in its similar-sized and contemporary cousin, *Chilotherium*. *Teleoceras* probably had a nasal horn; it may have had sinuses in the nasal bones. This may be true also of the Miocene *Diceratherium* which possessed a pair of nasal horns. But all this has not been investigated. With regard to the roles played in the causation of frontal sinuses by horns, by skull size, and by vaulted cerebral hemispheres, it is deplorable that the skull of the Upper Oligocene hornless giant *Baluchitherium* is now a reconstructed exhibition specimen. A longitudinal section was drawn when the skull was under investigation (Granger and Gregory 1936, pl. II), but no details of bone structure are shown. Presumably no details were recognizable in this unique specimen.

Let us realize, here at the end of our survey of frontal sinuses in Tertiary mammals, that the record is poor not alone because interest in pneumatization may have been lacking. Relatively few fossil skulls are — as found, without intentional sectioning — appropriate material for such studies.

4. The Equidae

We have digressed from our own story, that of frontal sinus evolution in the Equidae. A survey of pneumatization and its possible causes in other mammals was necessary as a general setting for our one case and as an aid in its interpretation. All other special studies in pneumatization, concerning as they do the extant mammals, are based on specimens more satisfactory than our fossil ones. Our specimens, however, have the advantage of being from consecutive geological periods, and they constitute a phyletic series, including the earliest form recognizable as an equid.

The material studied consists of crania and endocranial casts which had been assembled for brain studies. The immediate impression obtained from this series of specimens was that expansion of the anterior cerebral region — and thus of the braincase — was the major factor in disturbing the original harmony between the surface of the skull and the organs encapsulated within the skull; that, consequently, progressive brain evolution was the main cause of the intra-cranial incongruities in which the frontal sinus developed. However, the survey of frontal bone pneumatization in other mammals showed sinus formation to be influenced by the specialization of this, or another, or several elements of the skull, by skull size, the size and even the general constitution of the body. Inside the skull of the Equidae, expansion of the cerebrum is the evolutionary process which happens to have been studied step by step in a special investigation. The other factors likely to participate in the causing of pneumatization must now be considered.

The gains in body and skull size failed to induce skull roof pneumatization up to the early Miocene. We have seen the interior matter of the frontal bone loosen up in the late Oligocene and early Miocene, preliminary to cavity formation, and size must be presumed to have played a role in this process. However, no sinus was formed in the Lower Miocene *Parahippus* MCZ 17878, a skull far larger than that to which belonged the Middle Miocene *Merychippus* fragment AMNH 32671, the oldest of our specimens which contains a frontal sinus. But size certainly was a factor in the later expanding of the sinus; with the skull's enlargement, discrepancies present must have grown, whatever had been their original cause. Further, the chief evolutionary change in the equid skull was one correlated with the successive increase in body size: the increasing preponderance of the facial skull, i.e. masticatory apparatus + nasal tunnel, over braincase + orbits.

The authors who studied this transformation have studied the changing length proportions. For the detection of disharmonious development in the frontal sinus region more and different measurements would of course be necessary. Presumably it has been regarded as superfluous to study the manner in which facial and cranial heights and breadths have increased; while the skull enlarged, its shape appears to have remained very much the same except for the change in pre/post-orbital length proportion. Still, a necessarily brief comparison of breadth and height differences between *Hyracotherium* and *Equus* may be of interest in the present context, if only to show how great was the expansion of the skull in 55,000,000 years of horse evolution.

The specimens measured are the *Hyracotherium venticolum* type skull (in Cope's pl. 49^a, 1884), and the two *Hyracotherium* fragments and 2½ *Equus* skulls at hand. While skull length changed from 135 to an average of 583 mm (1 : 4.3), neurocranium breadth increased from 28 to 122 mm. (1 : 4.4). In height the neurocranium gained less, from 32 to 113 mm. (1 : 3.5), but the facial skull gained more. At the infraorbital foramen, muzzle height in eohippus AMNH 14810 is 28 mm. (above P^4), in the three *Equus* 140 (above P^4), 135 (above M^1) and 150 (above M^1), respectively, so that *Hyracotherium* compares to the *Equus* average as 1 : 5.1. The mean of the posterior and anterior height ratios is 1 : 4.3. This number may be the result of playful juggling with a few figures, or it may be found to be the height increase ratio of the main frontal sinus region which is in a position intermediate between those of the two height measurements taken. The length, breadth and height ratios arrived at in the present rather unreliable manner are certainly amazingly similar. A different kind of material indicates that an elongated muzzle is not in itself a factor creating or enlarging a frontal sinus; in the hippopotami (fig. 5) it is the shorter-faced type which has the larger sinus.

In fossil and living mammalia the development of skull superstructures is generally correlated with body size. Crests in particular are a feature of large animals which is lacking in smaller related forms, and they are known as a factor in pneumatization. As mentioned above (p. 427) there is nothing comparable in the ancestral series of the Equidae. The trend in equid evolution was the opposite of that generally observed. The small *Hyracotherium* had a rather conspicuous medio-sagittal crest on eight-ninths of the length of the cranium. A lower crest was on five-eighths of the cranium of *Mesohippus* — naturally, with some variation. Definite crests of variable extent and strength occur in *Miohippus, Parahippus,* and in *Merychippus* where I found it one-half the length of the cranial roof. One-half seems the rule also in *Equus;* but in this largest of the Equidae, which has the largest frontal sinus, the original sagittal crest has dwindled to "a more or less prominent line" (Sisson 1940, p. 57). It seems that in *Equus* a crest had become superfluous; the wide and high cranial box alone is large enough to provide a sufficient surface for the attachment of the extensive head muscles.

One external structure enlarged considerably, and changed in shape and in relative position, with the enlargement of the equid skull. The postorbital process of the frontal bone is a mere stump in *Hyracotherium.* It joins the frontal process of the zygomatic bone only in the *Merychippus* stage of horse evolution. The postorbital bar thus formed is slender in some, broader in other *Merychippus* specimens, and since this stage it has increasingly become a more voluminous structure. In *Hyracotherium* the interior of the postorbital process consisted of cancellate bone tissue; the bar in *Equus* is pneumatized. The expansion of the process has considerably added to the frontal bone but outside the cranial circumference. The process was invaded by the sinus; but has it contributed to its origin? (One may note that the extremely pneumatic pig skull has only a postorbital stump.) Knowledge of the internal structure of the postorbital process of *Merychippus* frontal bones might help to decide this question.

The anterior rim of the postorbital process or bar is the posterior border of the orbit. The phylogenetic shift of the anterior orbital border is a much-studied, well-established fact. I found the posterior border of the orbit remarkably conservative in its relation to the structure it adjoins medially, viz., the constriction of the cranium which marks the anterior end of the cerebral capsule. Only in *Hyracotherium* is the postorbital process anterior to the cranial constriction.

Since the *Mesohippus* stage, cranial constriction and postorbital process have occupied the same transverse skull region; in *Equus* the plane of the constriction is generally that of the posterior border of the process. (My remarks 1948, p. 117, on certain topographical changes in this region, refer to the anterior extremity not of the cerebral capsule but of the braincase, the location of the cribriform plate.) The transverse skull region at the anterior end of the cerebrum is that in which, as we have seen, the frontal sinus originated in *Merychippus* and has its greatest diameters in *Equus*. Therefore it is interesting that this region was always broadened dorsally by the postorbital process of the frontal bone, long before the stage in which the nucleus of the frontal sinus developed and the process contacted the zygomatic bone.

The great preorbital changes of the equid skull thus appear to be hardly reflected in the posterior region of the orbit. This suggests that the conspicuous "backward shift" of the orbits was no factor in the causation of the frontal sinus proper. The shift was rather a change in the topography of more anterior skull regions. A survey of published figures shows the anterior border of the orbit above M^2 from *Hyracotherium* to *Miohippus;* in *Parahippus* the same or above the anterior end of M^3; in *Merychippus* and *Pliohippus* above M^3 or its posterior end; in *Equus* the entire dental region is "removed" from the orbital region. This process in horse evolution must have given the maxillary sinus considerable possibility, or cause for enlargement. The lateral, orbital sections of the frontal sinus must also have been involved in the process; but a direct influence of this preorbital reconstruction on the mainly postorbital frontal sinus proper seems highly improbable.

Has the expansion of the olfactory organ, so much greater than that of the brain, produced discrepancies which called for pneumatization? One cannot simply take as an affirmative answer the fact that mammals with reduced olfactory organs have no frontal sinus (Cetacea, etc.) or a small frontal sinus (*Homo*). Not only have macrosmatic lower mammals unpneumatized frontals, too, but in all these forms the skull structure is so utterly different from that of the horses that such comparisons teach nothing about frontal sinus development in the Equidae. In equid evolution ethmoidal labyrinth and braincase actually have extended their contact more than would correspond to their general enlargement. As in living mammals with a primitive type of brain, the nasal capsule adjoined the braincase anteriorly in *Hyracotherium*. It was mainly in front of the brain in the *Mesohippus* stage; only the posterior extremity reached back below the olfactory bulb chambers (fig. 2). With progressive evolution the cribriform plate comes to face downward as well as forward and, concomitantly, the nasal capsule extends posterad. Thus one finds in *Equus* a pars subcerebralis added to the original, precerebral labyrinth (fig. 3A). Dorsally, however, this same progressive evolution does bring about a discrepancy between braincase and ethmoidal labyrinth: through the relatively low position of the brain part of the olfactory organ, the bulbi. This, we believe to have shown above (and1948, p. 145–146), is the result of the progressive expansion of the cerebrum.

Has the masticatory apparatus played a decisive role in frontal sinus formation? A remote relation no doubt existed, because the formation of hypsodont teeth, of the frontal sinus, and an anterior vaulting of the cerebrum all are features started during the Middle Miocene reconstruction of the equid skull. They must have been correlated insofar as none of them basically changed the shape of the skull, although they are manifestations of different trends — higher crowned teeth an adaptation, to the hard grasses which first appeared at just this time (Stirton 1947, e.g., p. 36) — cerebral expansion the result of a force largely independent of body evolution — sinuses originating in discrepancies caused by unharmonious evolution of the skull components. Possibly, knowledge of the anterior extent of the frontal sinus in *Merychippus* will aid in distinguishing between the influence on the frontal sinus of the teeth, anteriorly, and the brain, posteriorly. The following conditions in Recent mammals are perhaps significant in this respect. The hypsodont, low-brained rodents generally have no frontal sinus (it is recorded only in the peculiar skull of *Hystrix*, and the large forms *Myopotamus* and *Hydrochoerus* — Paulli 1900, p. 516, 517, 521). The brachyodont *Tapirus* has considerable frontal sinuses in front of its high cerebral capsule (Paulli 1900, fig. 2).

Data on the possible role of hypsodont teeth on the one hand, and the role of the braincase on the other hand in the evolution of the equid frontal sinus, can presumably be found in the Mio-Pliocene "forest horses". In this side-branch of the *Equus* ancestry a progressive feature is the high and rounded braincase, while among the many primitive features are persistently brachyodont teeth. "The development of large frontal sinuses" was recorded by Scott (1895, p. 97) in the type of *Hypohippus equinus;* but this statement was based on an error. The specimen contains only two identifiable fragments of the cranium — one an ear region, the other a part of the left and dorsal cranial wall. The lateral processes at the anterior and posterior ends of the latter fragment are shown in Scott's side view reconstruction of the skull (loc. cit., pl. III, fig.23) enclosing the orbit; they are, however, the zygomatic processes of the temporal and frontal bones (as which they are rightly described loc. cit., p. 97). The cavity which Scott saw on the medial side of this fragment was, consequently, not a sinus but it belonged to the cerebral chamber. Dr. Jepsen had kindly cleaned of matrix the inside of the specimen before I studied it. Impressions of cerebral gyri are now easily seen and, further, a short stretch of the falx cerebri. *Hypohippus* may have had frontal sinuses, but not in the region preserved in this specimen (Princeton University no. 10404).

Thus discussing each element regarded as influencing frontal sinus formation in other mammals has only turned us back to that element the star role of which had been suggested by the equid material itself. All structures adjoining the sinus must have participated, through different developments and shifts, in shaping the sinus; in fact the "function" of the frontal sinus is to mediate between these structures. In none of these structures, however, have I found changes during equid evolution which could be regarded as decisive in originating the frontal sinus proper, except in the brain (p. 430).

The cerebrum has expanded and changed in form, in the evolution of the Equidae as of vertebrates in general, largely independent of body and skull size. Therefore, if the origin of the equid frontal sinus really was due to the evolutionary expansion of the anterior cerebral region and the concomitant relegation of the olfactory bulbs to a successively lower region of the skull, the origin of the frontal sinus proper is another feature in equid phylogeny not connected with the gradual size increase. Size increase, through the changes in skull size and structure related to it, has thereafter enlarged and shaped the frontal sinus proper as well as the orbital and turbinate pneumatic cavities which in *Equus* are parts of the frontal sinus s.l.

The origin of these latter cavities is a different story. It cannot be told from the material at hand — un-pneumatized orbit roofs of *Mesohippus*, and the endocast of what appears to be a small sinus anterior to the olfactory bulbs and medial to the orbit in *Parahippus* MCZ 17878. In ungulate ontogeny the Anlagen of the anterior sinus portions precede those of the frontal sinus proper; in an artiodactyl phylogeny we have seen supra-orbital sinuses developed before the frontal sinus proper came into existence. Seen historically, it seems probable that the air cavities in the anterior part of the orbit and in front of it were facial formations with a separate origin and with causes different from those which gave rise to the cranial sinus in the frontal bone. If this was the case, they have become secondarily, by confluence, the "anterior frontal sinus regions" as which they appear today in the morphology of the adult horse skull.

V. SUMMARY

The frontal sinus of *Equus caballus,* frequently described in the literature, was studied with particular regard to the structures it adjoins. The deepest and broadest sinus area overlies the anterior slope of the cerebral chamber and envelops from above and laterally the olfactory bulb chambers. It tapers out over the ethmoidal labyrinth, but except for this anterior region in the nasal it is within the frontal bone, a frontal sinus sensu stricto. The frontal sinus of current nomenclature includes latero-anterior cavities with which the main cavity is continuous; these pneumatize the wall and roof of the orbit and a posterior portion of the dorsal turbinate.

The area corresponding to that of the frontal sinus proper was studied in crania of some fossil Equidae. The sinus did not exist in the early ancestors of the horse. In its place, Lower Eocene to Middle Oligocene skulls have small-celled cancellate bone, Upper Oligocene and Lower Miocene specimens a more extensive layer of coarser spongiosa. The first frontal sinuses were found in a Middle Miocene representative of the genus *Merychippus.* This small phyletic Anlage developed in that section of the skull in which the Recent cavity is widest. The frontal sinus of *Merychippus* lay laterally over the anterior slope of each cerebral hemisphere and olfactory bulb, while the median region of the frontal bone was not yet pneumatized.

From a survey of the various evolutionary changes observed in the equid skull it is concluded that cerebral expansion was the decisive factor in the origin of the frontal sinus. In the *Merychippus* stage the equid cerebrum first developed an anterior facies which rose considerably above the bulbi. This created a major discrepancy between the tabulae externa and interna of the frontal bone, and the unoccupied space was invaded by air. In the evolutionary expansion of the sinus other factors came into play besides increased anterior vaulting of the cerebrum. Enlargement of the head in particular caused and enlarged discrepancies between the elements of the skull, that is, spaces not used and therefore subject to pneumatization.

This story of the equid frontal sinus agrees with Weidenreich's theory of sinus origin and evolution, deduced from extant conditions. Sinuses have no function. They occupy dead spaces which have resulted from disharmonious growth of the skull components, viz., the capsules of brain and sense organs, the tooth apparatus, and the outer plates of the skull.

Also in agreement with this concept is the general impression obtained from a survey of frontal bone pneumatization in the extant mammals. Its infinite variation is baffling; from this fact alone it can be deduced that there is no one explanation for all the differences. In general it is true that larger skulls are more extensively pneumatized than small ones of comparable build; but not even size differences have in different groups the same correlation with the extent of pneumatization — enlargement of a skull cannot ever have been a congruent enlargement of all the skull elements. In a number of cases one easily sees the relation between size of sinus and arrangement of skull components; a frontal bone horn, for example, has lifted the cranial roof plate from the braincase, and the resulting incongruity between the tabulae externa and interna was pneumatized. Recent heads, however, can rarely reveal the actual origin of the pneumatized discrepancies within the skull. It is obvious that there are many possible causes of origin and expansion of frontal sinuses, and they must have been different in different phylogenies.

Such different causes, and conditions in early Tertiary mammals strikingly different from those in roughly comparable Recent forms, are brought to light in a survey of paleontological data. Most of these findings are chance observations on chance breaks — cavities or sinus endocasts accidentally, and in general only partly revealed. Sectioned fossil skulls have rarely been used for sinus study, and serially sectioned skulls never. In almost no genus have sinuses been noted in more than one specimen — and individual variability is particularly characteristic of sinuses. Very few of the genera studied are phyletically connected. On such data rests the following summary of frontal sinuses in Tertiary mammals. It is brought together from the literature and the author's studies of Eocene and Oligocene specimens.

In toxodonts a frontal sinus was present from the Upper Eocene onwards; the earliest was associated with a peculiar downward bend of the anterior brain region which bent the inner plate of the frontal bone away from the outer plate. An armadillo frontal sinus is reported from as early a time as the Lower Eocene, and from the same strata a domed, pneumatic forehead of an astropothere is known. Quite recently a Paleocene frontal sinus has been discovered; it pneumatized a small part of the enormously thick skull roof, from the anterior brain region forward, in a large pantodont. To judge from the other data known, such early occurrence of frontal sinuses was exceptional.

One genus of Oligocene Canidae lacked the frontal sinus; another developed a short, low cavity; but this was well developed in larger, Miocene and Pliocene forms with a domed connection of cranium and muzzle. A Middle Oligocene artiodactyl, whose orbit roof was pneumatic, had no frontal sinus proper; an Upper Oligocene, larger descendant developed a sagittal crest and below this the supra-cerebral sinus. In Eocene, Oligocene and some Miocene Rhinocerotidae no sinuses could be found; at least one Upper Miocene hornless genus had the wide pneumatic cavities comparable to those of extant rhinos except that the nasal bones were not involved; clearly it was the development of the horn base through which Pleistocene and Recent forms have added sinus compartments in the nasal bones, to arrive at their extreme pneumatization of the entire skull roof.

This condition in the extant perissodactyl giant contrasts notably with that in the extinct archaic groups of rhino-like habitus and size, the Middle Eocene uintatheres and the Lower Oligocene end-forms of the titanotheres. The bones of their gigantic heads were largely massive. Their enormous bony horns were invaded by diverticula from adjoining sinuses, but these hardly ever reached beyond the horn base. *Uintatherium* appears to have had, besides maxillary sinuses expanding into the bases of the middle horn pair, a pair of narrow air tunnels over the olfactory bulb chambers, extending into the bases of the posterior horns.

Pneumatization in the titanotheres is better documented; we have data not from one but from three stages of the early Tertiary. The Middle Eocene *Palaeosyops* was the size of a very large tapir. It had a frontal sinus proper over the bulbi and anterior cerebrum, plus a lateral sinus at the postorbital process. Nevertheless the skull roof, which was very thick, consisted mainly of bone. The pneumatized areas were far smaller in *Palaeosyops* than they are in tapirs. There is, further, a great difference between the skulls of the Middle Eocene and the Recent perissodactyl with regard to the size of the brain capsule. The large head of *Paleosyops* was developed at a time of mammalian history in which cerebral expansion was in a slow stage and brains of large mammals were, consequently, small. It seems that frontal sinus expansion likewise did not keep step with skull enlargement in the manner known in present-day mammals. In *Palaeosyops*, as in the contemporary *Uintatherium*, and in the Paleocene *Haplolambda*, the vast roof of the small brain chamber contains a sinus only in the lower half of its anterior region.

This condition was still present in the Lower Oligocene descendants of *Palaeosyops*. The brain capsule of these later titanotheres was a huge mass of solid bone. A restricted frontal sinus existed, mainly in the olfactory bulb region, nowhere pneumatizing the median areas of the roof, which are solid bone. The sinus extensions are dorso-lateral only. We have found a short one posteriorly, a long one anteriorly, and diverticula into the bases of the horns — except in the case of terminal horns: these are solid. In these titanothere skulls neither the attainment of giant size nor the development of gigantic superstructures stimulated pneumatization in the manner which in Recent mammals is almost a matter of course. Today, a thick and massive cranial roof exists only in the Sirenia, an order which apparently at no time possessed frontal sinuses. The late titanotheres had this in common with the sirenians that their limb bones, too, were massive; there may have been a similar trend, counteracting the extension of pneumatization. Their cranium was, however, far larger than that of seacows, absolutely as well as in relation to the brain. Instead of enlarging in correspondence with its original and main function, that of being a brain capsule, this cranium enlarged in correlation with the general enlargement of the body — and the resulting discrepancies were, in the greater part of the cranium, not pneumatized. Only one ancient mammal seems to be known in which such a wide supra-cerebral space was pneumatic, and this was another titanothere, *Dolichorhinus* of the Upper Eocene. Only of one ancient mammal do we know hollow horns — the giant Lower Oligocene *Arsinoïtherium.* Today, all bony horns are hollow. Up to 35 million years ago, this condition was exceptional.

During the search for cranial frontal sinuses it was incidentally observed that sinuses in the orbit walls may exist in a phyletic stage preceding the development of the frontal sinus proper. Orbital sinuses, consequently, can be independent developments; indeed they are the only dorsal sinuses in small living artiodactyls. Seen historically, they are not necessarily expansions of the cranial frontal sinus as which they appear in present-day topography of, for example, the horse skull. Further it was found that maxillary sinuses were in fact an early acquisition in mammaliam phylogeny, as their general occurrence and early Anlage in living forms had suggested. A maxillary sinus was present in the Eocene even in cetaceans, in whose later representative it is absent; and in the Equidae it was present in *Hyracotherium,* 30 million years before their frontal sinus developed.

It is, of course, foolhardy to draw general conclusions on the basis of data such as were available for the present study — e.g., a "series" consisting of three Oligocene, one Miocene and one Pliocene individual out of millions of fossil Canidae. The discovery (in great part on previously published specimens) of two fundamentally different evolutionary developments in two branches of the titanotheres has highlighted the fact that there is much material in our collections which has gone uninterpreted with regard to sinuses; further, as the condition in the titanothere giants may be either primary or secondary, the case exemplifies the fact that even a relatively well documented pneumatization story is open to several interpretations. I cannot, however, resist the temptation to describe a general picture of frontal sinus history which I gained from other authors' and my own observations.

Development of a frontal sinus relatively late in phylogeny has occurred in many phyla. Frontal sinuses were rare in the early Tertiary and only later became that characteristic of mammals which they are today. No frontal sinus was developed in Eocene and Oligocene representatives of orders in whose Recent genera the frontal bones are pneumatized. Bony horns were not in general pneumatic before the Miocene.

One has, of course, to consider the relation between the size of a skull and its pneumatization. We have seen one skull element, the brain capsule, not enlarging pari passu with phyletic enlargement of the head, and the same is true of at least two other elements, the capsules of eye and ear. Further, large superstructures of the head are in general peculiar to large forms. Thus discrepancies within the skull are bound to develop with phyletic size increase, and one reason for the increasing occurrence of frontal sinuses is certainly the fact that during the Tertiary body size increased in many phyla. This, however, is not the whole story. Discrepancies which are pneumatic in rhinoceros and elephant were not in general pneumatized in giant skulls of the early Tertiary; they were invaded by sinus diverticula only to a modest degree. Further, pneumatization is present today in similar-sized and smaller relatives of the early Tertiary forms in which it was absent.

The comparative rarity of frontal sinuses in the early Tertiary can be explained by, and is an evolutionary support of Weidenreich's theory of sinus origin. The early representatives of the surviving orders were more primitive than are the living genera. In the original mammalian condition, the skull components must have harmonized. There were no discrepancies between the brain chamber, the capsules of the sense organs, and the cranial surface — hence no room nor reason for frontal sinuses. The primitive mammal skull was designated to encase the sense organs as inherited from the Reptilia, and a brain which, with its portions serially arranged on one level, was not yet basically different in shape from the reptilian brain. This probably accounts for the fact that absence of frontal bone pneumatization can be added to the list of primitive characters in Mammalia. The early acquisition of maxillary sinuses is presumably related to the definitely un-reptilian masticatory apparatus of even the earliest mammals.

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Explanation of Abbreviations

C., cerebral chamber
E., ethmoturbinals
O., olfactory bulb chamber
P., pit in sinus floor
S., frontal sinus
T., dorsal turbinal
f.m., fronto-maxillary opening
i.f., infraorbital foramen
n.c., nerve canals
or., orbit
p.f., postorbital foramen
se., septum sinuum frontalium
t., tentorium cerebelli

Page References to Figures